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The Effects Of Environmental Heterogeneity At Multiple Scales On A Community Of Five Diurnal Lemurs In Betampona Natural Reserve, Madagascar: A Landscape Ecology Approach

Emily Mertz
University of Colorado at Boulder, Emily.Mertz@colorado.edu

THE EFFECTS OF ENVIRONMENTAL HETEROGENEITY AT MULTIPLE SCALES ON A COMMUNITY OF FIVE DIURNAL LEMURS IN BETAMPONA NATURAL RESERVE, MADAGASCAR: A LANDSCAPE ECOLOGY APPROACH

by

EMILY MAURINE MERTZ

B.S., University of Missouri at Saint Louis, 2001

M.Sc., Oxford Brookes University, United Kingdom, 2004

M.A., University of Colorado at Boulder, 2006

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written by Emily Maurine Mertz
has been approved for the Department of Anthropology

Professor Herbert Covert

Professor Dennis VanGerven

Professor Matt Sponheimer

Dr. James Loudon

Professor Sharon Collinge

Date_____

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To understand a particular species' or community's response to forest fragments, the habitat attributes and the landscape pattern must first be quantified. However, methodology that identifies the influence of landscape pattern and local habitat structural attributes on species or community viability is poorly developed for non-human primates in fragmented forests. Successful primate conservation requires an understanding of how environmental variability at both micro- and macro-scales affects community structure and habitat use. The objective of this research was to identify landscape and local ecological characteristics that affect lemur community richness, abundance, and diversity using spatial analysis at multiple scales in Betampona Natural Reserve, Madagascar. This was accomplished through a landscape ecology perspective to document the effects of environmental heterogeneity on habitat use, behavior, and movement patterns among a community of five diurnal lemurs in a forest fragment. Vegetation structural analysis within forest patches, point-counts, and radio-collar-aided follows, in conjunction with Geographic Information Systems, were methods used to address the disconnect that has emerged involving the importance of landscape spatial pattern and primate extinction risk. The main conclusions of this research include: 1) the quantified patches demonstrate differences in micro – and macro-habitat attributes, 2) variation exists in lemur community structure and diversity indices within the patches, 3) point-count data suggest that micro- and macrohabitat features affect lemur resting, moving, and feeding behaviors, whereas radio-collar-aided follows indicate that macrohabitat has less of an effect on lemur behavior, 4) it is inappropriate to make broad generalizations based on a particular response of one population, one group, or even one individual primate to habitat alteration and extinction

risk with any degree of certainty, and 5) consolidating ecological and behavioral variation into a single category such as “fragmentation,” undermines the ability to identify correlates of extinction risk. The development of conservation methodology and building comprehensive data sets to understand how biodiversity utilizes its environment at multiple spatial scales is vital. These data will provide information for reforestation and corridor projects in an island nation where forests are disappearing, demanding conservation solutions that aim to reinforce the balance between development and biodiversity.

To Polly, Don, and Ryan

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CHAPTER 1
RESEARCH OBJECTIVES AND BACKGROUND

Research Objectives

The objective of my research was to employ a landscape ecology perspective in conjunction with forest fragmentation research to document the effects of environmental heterogeneity on lemur species movement and community structure patterns at both local and landscape spatial levels in Betampona Natural Reserve (BNR), Madagascar. This research focused on a community of five diurnal lemur taxa[1] (*Varecia variegata*, *Propithecus diadema diadema*, *Eulemur fulvus albifrons*, *Hapalemur griseus griseus*, and *Indri indri*) that reside in this forest fragment. The concomitant use of technological advancements such as radio-collars in tandem with Geographic Positioning Systems (GPS) and Geographic Information System (GIS) Habitat Modeling are innovative approaches that aimed to remedy the disconnect that has emerged involving the importance of landscape spatial pattern and primate extinction risk. This technology provided the forum for a detailed analysis of the effects of landscape spatial pattern on lemur community viability in BNR with an aim to reinforce the balance between development and biodiversity.

I pursued these objectives because understanding the effects of landscape spatial patterns on biodiversity survival is critical to successful land management. Madagascar's forests are disappearing. To understand the response of a particular species or community to forest change, habitat attributes and the landscape pattern must first be quantified. However, methodologies that identify the influence of landscape configuration and composition, in addition to local habitat structural attributes on species or community viability is poorly developed for non-human primates in fragmented forests. The effects of the breaking-apart of the landscape and consequent heterogeneity independent of habitat loss has received little attention, is sometimes too small to detect, and in some instances has a positive effect on biodiversity (Fahrig, 2003). Quantifying

[1] Lemur is generally used to refer to all the Malagasy strepsirrhines throughout this dissertation.

variation in habitat use across the landscape and identifying habitat structural variables and patterns at a micro- and macro- level that may influence variation among primate taxa is essential to understanding primate community assemblages in different habitat types. This kind of research focus directly impacts conservation policy by contributing much-needed data sets for informed decisions pertaining to land development based on species habitat preferences and movement patterns, where to restore habitat, where to protect habitat, and where to build/maintain connectivity.

Outline of Dissertation

Chapter 1 provides a discussion of the current literature highlighting the disconnect that has emerged involving the importance of landscape spatial pattern and primate extinction risk. This chapter also emphasizes the importance and relevance of the interconnected topics of landscape ecology, heterogeneity, habitat quality, and concepts of fragmentation. In addition, chapter 1 presents the results of a literature review on the current uses of the term/concept of fragmentation by authors in the primatological literature and discusses the importance of incorporating a landscape ecology perspective in future conservation research. I also discuss the influence of habitat heterogeneity and quality on species and community sustainability, and the importance of documenting primate response variability instead of depending on a verbal attractor like the buzzword "fragmentation."

Chapter 2 discusses the methodology used to answer the main research questions of this dissertation. This research was a multi-scaled project that utilized the distinctive ecology of BNR as a template to conduct a natural field experiment in a complex rainforest environment. The goal of this dissertation was to understand the broad context of landscape spatial pattern and how this relates to lemur behavioral processes. The multifarious nature of the rainforest hinders the ability to control all of the variables. Accordingly, I developed a methodology in such a way that provided

some level of independent variables. This was accomplished through an in depth analysis of eight quantified vegetation patches. The patches therefore became a constant that were returned to on a regular basis in order to observe the diurnal lemurs utilizing the patch. But, where were the lemurs going when they were not in the defined patch? To answer this question, radio-collars were placed on eight lemur individuals in different groups from three lemur taxa. These different groups were part of all day follows on a rotational basis so that behavioral data could be collected, but also so the path of movement and use could be recorded via GPS. Towards the end of this research the locations in the landscape the different lemur groups frequented on a regular basis were quantified following the same methodology applied to the eight defined patches in order to identify keystone structures.

Chapter 3 provides a detailed assessment of the structural variation within BNR necessary for the development of a framework within which to work, while also effectively representing the spatial component of this research. Eight patches were defined and quantified that contain distinctive microhabitat, structural vegetative attributes. These patches also represent varying macrohabitat and landscape attributes (e.g. the guava, longoza, or primary forest pattern within or around the patch), which may also be important contributing factors to ecological processes. The purpose of establishing patches in different locations in the reserve was to quantifiably represent the heterogeneity of BNR to ultimately test for the effects of landscape composition and configuration on lemur occurrence. This chapter discusses the quantitative descriptions of each of the patches, highlighting the main components that define the patch as a collective, distinct spatial unit concurrently separating it from other patches within the landscape. The total number of trees of economic and ecological value was also quantified in each patch. The results indicate that there are in fact quantifiable differences between the patches within BNR. These patches demonstrate differences in microhabitat as well as macrohabitat of the internal patch and surrounding area. GIS was utilized here to create spatial maps of the quantified patches.

Chapter 4 discusses the differences in lemur community structure observed from using all-day fixed radius (50 meter) point counts within the quantified patches. This methodology was essential to determine if variation existed among different lemur taxa in their ability to utilize certain patches or the inability to use other patches within the landscape of BNR. This component of my research was important in documenting if there were differences in lemur species abundance, richness, and diversity and so that the concept of patch quality could be further investigated. This chapter reveals that there are differences in diurnal lemur community structure within the different patches of BNR. These data were also analyzed within a GIS in order to visually represent the occurrence of the different lemurs (and their behaviors) within the quantified patches.

Chapter 5 discusses the potential reasons as to why there may be differences in lemur community structure throughout BNR. This discussion was based on how the local vegetation attributes within a patch and landscape attributes affect lemur community structure. This was accomplished by presenting an analysis of the behavioral data recorded from each taxa of lemur that utilized the different quantified patches. A comparison was also made of the different lemur taxa occurring in the patch and the different substrates used for their overall activities (i.e. resting, eating, and moving). This provided insight into what the possible limiting factors were in each patch, which in turn may dictate the different lemur taxa using or not using a particular patch. This analysis demonstrated that it is inappropriate to reduce the complexity of the rainforest into a single variable and that this variable is not the same for all lemurs. This is important and allows the five diurnal species of BNR to continue to co-exist in a forest fragment. The lemur community in BNR has thwarted local extinction because of their ability to so efficiently partition their niches so as to avoid competition for resources, space, or keystone structures. Spatial pattern may impact the occurrence of lemur taxa throughout BNR with some lemurs (i.e. brown lemurs, sifaka, and bamboo lemurs) responding more favorably to environmental heterogeneity, whereas for others, such as

ruffed lemurs, this heterogeneity may be more detrimental. Quantifying the variation in lemur habitat use across the landscape and identifying habitat structural variables and patterns at a micro – and macrohabitat level has shown to be an important component in understanding the primate community assemblages in different habitat types throughout BNR.

Chapter 6 is comprised of two main goals. The first consists of reporting and analyzing the behavioral and positional use of different substrates by three radio-collared lemur taxa to help answer questions pertinent to the importance of small-scale attributes in patch choice. Ultimately this information is valuable for reforestation and corridor design. Substrates needed for a corridor project to increase movement behavior of the three lemur taxa is presented. The second component focuses on how configuration and composition affect lemur movement pattern in BNR. Does landscape spatial pattern and heterogeneity influence movement and habitat use for indri, sifaka, and brown lemurs? Radio collars were placed on eight lemur individuals in different groups from three lemur taxa and the methodology was followed as described in the overview of chapter 2. The results indicate that microhabitat affects lemur resting and moving patterns in BNR. Macrohabitat does not affect movement and habitat use among the radio-collared lemur taxa in BNR. Some lemur groups appeared confined to certain areas but this may be better explained as a result of social boundaries rather than landscape constraints.

Chapter 7 incorporates the results from chapters 3 to 6 into a discussion nested within the current literature. This chapter revisits the primary goals of this research, highlights the major findings, and discusses the strengths and weaknesses of the two methodologies used in this research. The main conclusions of this research are summarized below.

Main Conclusions

1. There are quantifiable differences between the patches within BNR. These patches demonstrate differences in microhabitat as well as macrohabitat of the internal patch and surrounding area.
2. There is variation in diurnal lemur community structure and diversity indices within the quantified patches of BNR.
3. Different scales of landscape pattern and heterogeneity affect the various lemur taxa and even single groups and individuals within the same taxon differently.
4. The research methodology employed may indicate either a higher importance of microhabitat or macrohabitat on different lemur taxa and groups. In this research, the point count results suggest that micro- and macrohabitat scale features affect lemur behavior and movement patterns, whereas radio-collared follows indicate that macrohabitat has much less of an effect on lemur behavior than microhabitat attributes.
5. It is unproductive to make broad generalizations based on a particular response of one population, or even one group of primates with any degree of certainty. The results from this research are a further example of how multidimensional factors may influence behavior and patch use patterns, population size, and extinction risk in a forest fragment. The variation that exists in response to different spatial scales and the associated co-variables (e.g. food distribution, social boundaries) creates a complex framework within which to implement effective conservation management.
6. Grouping complex ecological and behavioral variation into a single category called "fragmentation," undermines the ability to identify unknown potential correlates of extinction risk.

Introduction

Madagascar is ranked as one of the top priority biodiversity hotspots in the world due to an alarming rate of habitat loss, extinction risk, and high species endemism. The current extrapolated deforestation rate of 111,000 hectares per year suggests that the eastern rain forest ecosystem will be lost by the year 2020 (Irwin et al., 2005). A recent coup and subsequent political instability, driving Malagasy people further into poverty, has set the stage for environmental plundering at both the local and international level. The pressing need for economic growth compels Madagascar to allow destructive land development, which is often highly unregulated especially in light of the current political crisis. Primary forces driving local extinction events are hardwood extraction, international oil drilling and exploration, and mining operations. For example, a global mining firm, Rio Tinto, mines for ilmenite in the forests of southeastern Madagascar. This mining company will remove habitat in 50 hectare increments for the next 40 years. Additionally, Canada's Sherritt operates a nickel mine adjacent to crucial biologically-rich forest sites. The damage is already visible where Sherritt has cleared forest for open-pit mining as well as a 136-mile pipeline to deliver slurried laterite to the port city of Tamatave. Sherritt has attempted to build "bridges" above the pipeline as part of the "Lemur Management Plan" to allow lemurs to cross, offsetting the forest destruction. The establishment and infrastructure for the Ambatovy Nickel Mining Project began in 2007. The bridge projects however did not commence until 2009. Moreover, the bridge architecture does not appear to be based on lemur locomotion and behavioral data or the habitat structural characteristics that are vital in accommodating lemur travel and dispersal. In a recent paper (Mass et al., 2011), the authors allude to the advice of "lemur experts" in the building of the bridges with no citations or presentation of data that was used to accommodate the thirteen taxa of lemur that live in the surrounding forests. Suspension and plank bridges were built to primarily accommodate road width and vehicle traffic type width, suggesting that bridge use by the lemurs was more of an afterthought to cater to "emergency conservation" efforts. Lemur use of the bridges

is being monitored as part of a follow up plan and six of the thirteen taxa have been observed using the bridges, although those same taxa also use the ground to negotiate the gaps in the forest (Mass et al., 2011).

While habitat can be removed in various ways that creates different spatial patterns across the landscape, the focus of much primate research has been on habitat loss and not habitat heterogeneity and pattern masking the true effects of forest spatial configuration on primate viability or extinction. An important question is, does environmental heterogeneity affect movement and community structure patterns at different spatial levels (e.g. macro- and micro-habitat) and ultimately promote or prevent extinction risk? Based on the growing human population and Madagascar's need for economic growth we expect that large areas of intact forest will continue to be transformed into a mosaic of forested and deforested areas in the near future. The development of flexible working models *a priori* that focus on how land can be removed or even replaced in order to minimize extinction risk is mandatory for effective environmental policy and subsequent ecosystem sustainability.

BNR is one of the last remaining forests of eastern lowland rainforest in Madagascar and is threatened by anthropogenic pressures (e.g. slash and burn farming and invasive plant spread) that modify the landscape. As a result, the landscape is in various stages of re-growth generating identifiable patches that are different in habitat structure, topography, configuration, and composition throughout the reserve (Mertz and Sandberg, personal observations). The individual patches[2] in BNR are separated by a certain degree of matrix thus limiting connectivity, influencing ecological processes such as the movement and dispersal of organisms, resource use, and ultimately gene flow (Pearson, 1993). As such, the patch dynamics and biotic exchanges among patches, which determine the ecosystem structure and function, need be of major concern in the conservation and management of forest ecosystems (Lewin, 1984; Nagendra, 2001). By quantifying

[2] Landscapes are composed of multiple elements (or patches) and the variety of these elements creates heterogeneity within an area.

and defining eight select patch types in BNR for my dissertation research I developed a template with which to understand species movement patterns and differential patch use to assess the spatio-temporal variability in species distributions, productivity, and survival.

The dynamic primate community of BNR in conjunction with the patches of varying degrees of structural integrity and disturbance, presents an ideal opportunity to conduct a natural experiment resulting in empirical evidence regarding the affects of habitat disturbance on community based movement patterns in a fragmented environment. This is important because, although conservation science has focused on the ecological and behavioral responses of single species to forest fragmentation, the effects of fragmentation and landscape patterns on community dynamics (latitude of flexibility) are poorly understood, particularly among non-human primates (Cowlishaw and Dunbar, 2000). There have been few controlled experiments focusing on the effects of fragmentation independent of habitat loss (but see Lovejoy et al., 1986; Fahrig, 2003). The controlled experiments that have been conducted have focused primarily on small mammals and insects in environments that can be manipulated (e.g. grasslands) (e.g. Caley et al., 2001; Collins and Barrett, 1997) and computer simulation models (With and King, 1999). Landscape-scale fragmentation experiments are rare (Ewers et al., 2011). The magnitude and obvious conservation ethics involved in conducting large-scale, tropical forest landscape modification experiments impede our full understanding of ecosystem complexity. The distinctive ecology of BNR provides an ideal situation to understand in more detail the effects of landscape modification and heterogeneity. The development of this conservation methodology and building a comprehensive data set to understand how lemurs utilize their habitat at multiple spatial scales, with the aim to be empathetic to local land use but also maintain ecosystem sustainability, was the focus of my doctorate research.

This chapter provides a discussion of the current literature highlighting the disconnect that has emerged involving the importance of landscape spatial pattern and primate extinction risk.

This chapter also emphasizes the importance and relevance of the interconnected topics of landscape ecology, heterogeneity, habitat quality, and concepts of fragmentation. Specifically, landscape ecology aims to understand the effects of spatial pattern (composition and configuration) on process, and thus landscape ecology accounts for the relevant spatial scale defined by the organism (Turner, 2005). Moreover, landscape ecology extends beyond the single patch and addresses the entire landscape including elements of the matrix, the complex area between forest patches. The merger of conventional forest fragmentation research with the discipline of landscape ecology is highly applicable for this research given the need for the greater understanding of landscape composition, configuration, and heterogeneity and their effects on ecological processes in the study of non-human primates.

Heterogeneity, or spatial patchiness, is an important variable to quantify within the framework of landscape ecology. Species persistence patterns and population viability in modified, patchy forests depend on a detailed assessment of forest structure and the quantification of spatial heterogeneity (Haila et al., 1989, 1996; Niemela et al., 1996; Turner, 2005). Heterogeneity operates closely with patch quality because understanding why organisms occur where they do or move as they do in a landscape requires a consideration of variation in the patches or patch quality. It is difficult to define patch quality and it is also a challenge to understand why organisms occur in a particular spatial pattern and move through their environment as they do (Wiens, 2002). Further complicating matters, the quality of a patch and of the landscape has to be defined from the perspective of the species or process of interest. Species operating at the same spatial scale may have different perceptions of whether a given landscape is connected depending on their particular habitat preferences and their ability or willingness to cross gaps of habitat that is considered low quality. Patch choice may be based on a variety of patch features, such as resource levels, population densities, habitat structure, predation risk, parasite/disease avoidance, social interactions, or even the quality of the adjacent patch.

Given the growing focus on fragmented landscapes worldwide the concepts of "fragmentation" are also important to address. Fragmentation is a popular buzzword that I argue is used to create concern within the conservation community about the pending extinction risks of biodiversity. There is ecological evidence that fragmentation can have a positive or a negative effect that cannot always be explained by the responses of "weedy," habitat generalist species (Fahrig 2003). This is an important conclusion to also consider when evaluating primate responses that I discuss in this dissertation as well as the need to be more specific in our discussion of accurately reporting complex ecological processes and biological idiosyncrasies.

The focus of this dissertation is to address and discuss the transpiring disconnect that has emerged between landscape spatial patterns and primate extinction risk and to present the results of research conducted in a Malagasy heterogenous landscape emphasizing the importance of identifying landscape and habitat characteristics that affect lemur community structure and viability using spatial analysis and GIS modeling at multiple spatial scales.

Primary Goals of Research

1. To quantify and define the structural habitat variation in terms of landscape physiognomy (i.e. vegetation, patch isolation, boundaries) (Dunning et al., 1992) and composition (i.e. species dominance, structure) (Turner, 1989) specifically focusing on habitat inundated with the invasive guava plant *(Psidium cattleianum)*, areas of past agricultural disturbance evidenced by longoza (*Afromomum angustifolium)* and areas of secondary and primary forest collectively represented in a GIS landscape model.
2. To identify how attributes of patch and landscape spatial scale affect lemur communities in terms of species richness, composition, and relative abundance in BNR.
3. To identify how landscape small scale attributes (e.g. vegetation structure) in addition to patch configuration and composition affect lemur positional and correlated behavior as well

as movement patterns in BNR through radio-collared follows represented in a GIS landscape model. These data will be used to identify important habitat structures and to learn something about the process of habitat selection and movement. This information is useful for reforestation projects and diserning how to promote functional connectivity.

Background

Primates are remarkably well studied (e.g. Napier and Napier, 1967; Smuts et al., 1987; Rowe, 1996; Nowak, 1999; Campbell et al., 2010) with a growing conservation research focus in anthropogenically-disturbed habitats (Bernstein et al., 1976; Schwarzkopf and Rylands, 1989; Mittermeier et al., 1994; Eudey, 1995; Oates, 1996; Rylands et al., 1997; Cowlishaw and Dunbar, 2000; Ganzhorn et al., 2003; Marsh, 2003; Arroyo-Rodriguez and Dias, 2010, Irwin et al., 2010; Schwitzer et al., 2011). Human impact on natural ecosystems is the primary force driving local extinction events (Lubchenco et al., 1991; Millennium Ecosystem Assessment, 2005). As such, it is challenging to conduct primatological research without incorporating or acknowledging some aspect of conservation both for local communities and biota. Understanding and predicting the impact of human behavior and modification on biodiversity is therefore increasingly important to the future survival of ecosystems, as human activity is a dominating presence in ecological communities. Because of this augmented impact on landscapes, much attention has been directed towards habitat loss, modification, and fragmentation and the consequent effect on species survival and population viability (Bernstein et al., 1976; Fagan et al., 1999; Cowlishaw and Dunbar, 2000; Ganzhorn et al., 2003; Marsh, 2003; Henle et al., 2004). It is particularly important to understand the effects of fragmented patterns and the dynamics of small populations (Cowlishaw and Dunbar, 2000). A decrease in population density causes a species to become more vulnerable to local extinction (Terborgh and Winter, 1980), with the removal of just one or two individuals from a small population being detrimental (Britt et al., 2003a). In addition, even though further

degradation of a fragment may cease, the species inhabiting that remnant may still be confronted with possible extinction through environmental, genetic, and/or demographic stochasticity (Shaffer, 1981; Lande, 1998), especially species that occur naturally at low abundances (Davies et al., 2000). This may lead to some species disappearing locally, regionally, and eventually globally (Henle et al., 2004). Management recommendations for such species confronted with the above risks require research directed towards evaluating the capability and limits of an ecosystem to sufficiently support a population (Pimm et al., 1988; Jonsson and Ebenman, 2001; Drechsler, 2004; Henle et al., 2004). It follows that field research is vital as it provides data applicable for the synthesis of formal models that explain the mechanisms by which habitat modification influences or evades primate populations (Drechsler, 2004).

Despite wide discussion, the manner by which fragmented habitats affect the dynamics of small populations is largely unknown (Cowlishaw and Dunbar, 2000, Irwin et al., 2010). In our efforts to implement effective conservation management and to also better understand the biology of extinction both among extant populations and also past populations, it is important to understand those very variables that both allow viability or promote extinction. Remarkable flexibility has been observed within the order Primates regarding the ability of individuals to cope with habitat loss through a variety of behaviors (Viveiros de Castro and Fernandez, 2004; e.g. *Varecia variegata*, White et al., 1995; *Ateles*, Ferrari et al., 2003; Chaves et al., 2011; *Colobus guereza,* Thomas, 1991; Plumptree and Reynolds, 1994; *Procolobus rufomitratus*, Wahungu et al., 2005; *Cercocebus galeritus galeritus,* Wieczkowski, 2004; Wahungu et al., 2005; *Alouatta palliata*, Estrada and Coates-Estrada, 1996; Cristobal-Azkarate et al., 2005; Arroyo-Rodriguez and Dias, 2010; *Cebus apella*, Michalski and Peres, 2005; *Callicebus moloch*, Ferrari et al., 2003; Michalski and Peres, 2005; *Chiropotes satanas*, Boyle and Smith, 2010). For example, *Alouatta palliata* has been observed traveling distances of 10 to 200 meters to reach different fragments and can exist in areas of anthropogenic vegetation (Estrada and Coates-Estrada, 1996). Further, some populations are

capable of altering their diet and home range size (Galetti et al., 1994; Onderdonk and Chapman, 2000). Tana River colobus (*Procolobus rufomitratus*) are capable of residing on the forest edge (Wahungu et al., 2005) and can consume young leaves found in degraded secondary forest (Mbora and Meikle, 2005). Further, *Cercopithecus mitis stuhlmanni* consumes more unripe fruit as a primary resource in logged environments versus unlogged forest (Fairgrieve and Muhumuza, 2003). In conjunction with ecological flexibility, the ability of *Cebus apella* to thrive in degraded habitat (Wallace et al., 1998) is also due to a flexible social structure and an ability to maintain stable home ranges near urban settlements and agricultural mosaics (Michalski and Peres, 2005). We also see variability in social groups and mating systems that accompany changes in resource availability and distribution (Grassi, 2006). *Alouatta pigra* and *Colobus guereza* form smaller social groups in fragmented environments (Onderdonk and Chapman, 2000; Estrada et al., 2002) and *Presbytis entellus* exhibit one male groups with multiple females in disturbed areas, and multi-male multi-female groups in areas with less disturbance (Hrdy, 1977; Ross and Strivastava, 1994). *Hapalemur griseus alaotrensis* exhibits both pair bonded family groups as well as single male, multifemale groups in a single habitat (Mutschler et al., 1998; Nievergelt et al., 2002). *Hapalemur griseus* at Ranomafana National Park also show variability in density and group size depending on microhabitat differences and disturbance levels (Grassi, 2006).

Moreover, when the pressures of the past that caused extinction events are compared to present day incidence patterns of Madagascar's primate community, for example, the results indicate no simple, uni-causal explanation shared by extinct megafauna and extant lemurs (Godfrey and Irwin, 2007). Where hunting pressures may have been a primary force contributing to local extirpations in the past, extant lemurs currently residing in Tsinjoarivo suffer more from dietary limitations (Godfrey and Irwin, 2007). Given the diverse multi-faceted behaviors we observe in primate species, populations, and individuals, it becomes difficult to fully understand the latitude of flexibility concerning primate ecological aspects and demography that allow the persistence of

some primate taxa over that of others in anthropogenically modified landscapes (Ehardt et al., 2005).

Predicting ecological aspects that determine the abundance, or rarity, of particular primate species has proven difficult, and in some cases, despite the search for generalizations, no specific patterns can be elucidated (Chapman et al., 2005). Understanding the variation observed among species and the changing environment can be infinitely complicated, requiring great precision and contextualization on the type of destruction in each particular situation. Furthermore, if variation exists regarding the different factors and responses that cause particular species to be rare, "lumping" them together under one category undermines unknown correlates of risk (Owens and Bennett, 2000). Incidentally, the search for a simple cohesive explanation (e.g. the over-use of the term fragmentation) to explain, or define, the cause of complex biological phenomena is inconsequential. Research directed towards habitat fragmentation, destruction and modification is, however, particularly important given that some of the most threatened primate communities now survive only in varying degrees of fragmented forest habitats (Cowlishaw and Dunbar, 2000; Ganzhorn et al., 2003; Marsh, 2003). Understanding complex phenomena underlying primate flexibility to subsequently inform effective conservation adaptive management first requires distinguishing the basic concepts of habitat loss and habitat fragmentation.

The processes of fragmentation and habitat loss are serious threats to the continued existence of regional and global biodiversity (Wilcox and Murphy, 1985; Ehrlich, 1988; Saunders et al., 1991; Groombridge, 1992; McIntyre and Barrett, 1992; Ehrlich, 1995; Dale and Pearson, 1997; Law and Dickman, 1998; Laurance, 1999). As such, there is a massive research effort and body of literature targeted at evaluating the effects of habitat fragmentation on biodiversity (e.g. Laurance and Bierregaard, 1997 and references therein). The extensiveness of this literature is only rivaled by its diversity (Fahrig, 2003). Various researchers measure and evaluate the process of fragmentation in many different ways, resulting in different conclusions regarding both the

magnitude and response (positive or negative) of biodiversity (McGarigal and Cushman, 2002; Fahrig, 2003). Because of the diverse and vague use of the concept of fragmentation within the ecological literature, the value of this term has recently been called into question (Haila, 1999, 2002; McGarigal and Cushman, 2002; Villard, 2002; Fahrig, 2003).

I argue that the focus of much primate research has been on habitat loss and not fragmentation *per se.* The vague use of the concept of fragmentation suggests that the effects of different spatial configurations and the delineation of habitat heterogeneity across the landscape on primate species persistence remain largely unknown, which has important implications for the direction of future conservation endeavors and will significantly contribute to anthropological research.

Landscape ecology is the study of how landscape structure affects the abundance and distribution of organisms (Fahrig, 2005) and with biodiversity hotspots (*sensu* Meyers et al., 2000) rapidly shrinking in area, synergistic spatial analyses are essential to understanding spatiotemporal relationships between species and their environments. Furthermore, an analysis of the natural biology of fragmentation events will provide insight into primate adaptation and the differential success rates of various taxa of living and extinct populations. Identifying patterns of extinction and why species differ in susceptibility risk is important for conservation biology but is also fundamental to understanding the process of evolution.

Fragmentation and habitat loss

Forest fragmentation is frequently used synonymously with habitat loss, thereby making these two terms inseparable and conceptually ambiguous (Fahrig, 1997; Haila, 1999; Haila, 2002; Fahrig, 2003; Collinge, 2009). An important area of recent ecological research focuses on disentangling the effects of habitat composition (the amount and kind of habitat) and landscape configuration (the spatial arrangement of the habitat), emphasizing that these two terms are not

synonymous (Fahrig, 1997; McGarigal and Cushman, 2002). Although habitat loss does accompany habitat fragmentation to a certain degree, they are different phenomena and should be distinguished from one another.

Habitat loss is defined essentially as a reduction in the amount of habitat in a landscape (Figure 1A) (Fahrig, 2003). In contrast, habitat fragmentation is a landscape-scale process in which habitat is progressively subdivided into smaller and more isolated fragments (Figure 1B) (McGarigal and Cushman, 2002). A forest fragment is therefore a patch of native vegetation around which most or all of the original vegetation has been removed and converted to other uses (Saunders et al., 1987). Habitat fragmentation is a complex process and involves four main simultaneous quantifiable effects: a reduction in the amount of habitat, an increase in the number of patches, a decrease in the size of habitat patches, and an increase in the isolation of patches (Fahrig, 2003). However, the inter-relationships between these measures are not widely recognized with most researchers focusing on one or two, but rarely all four, thus making the interpretation of the results and comparison with other studies difficult (Fahrig, 2003). Forest fragments also result in higher edge to interior ratios, fluctuations in energy balance, and increased isolation over time that results in decreased dispersal and thus gene flow (Saunders et al., 1991; Gehring and Swihart, 2003). Specifically focusing on habitat loss, empirical evidence does indeed indicate consistent negative effects on biodiversity in terms of population growth rates (Bascompte et al., 2002; Donovan and Flather, 2002), species interactions (Taylor and Merriam, 1995), dispersal success (With and Crist, 1995; Pither and Taylor, 1998; With and King, 1999; Belisle et al., 2001), genetic diversity (Gibbs, 2001), species richness (Wesstein and Schmid, 1999; Schmiegelow and Monkkonen, 2002) and population abundance and distribution (Lande, 1987; Venier and Fahrig, 1996; Gibbs, 1998; Guthery et al., 2001).

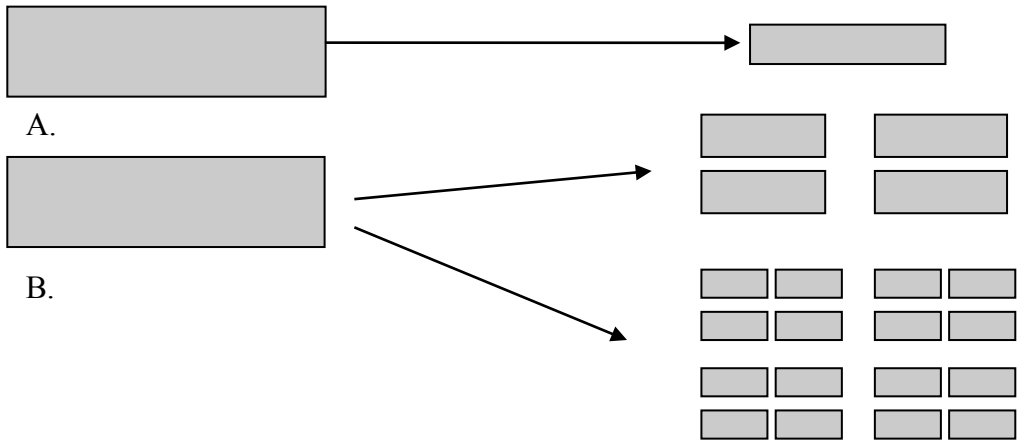

Figure 1.1 Illustration of habitat loss (A) versus habitat fragmentation, the breaking apart of habitat independent of habitat loss (B)

When the negative effects of habitat loss on biodiversity are extended to the term fragmentation, the latter is then also viewed negatively and associated with a decline in flora and fauna (Fahrig, 2003). However, fragmentation effects are exceedingly difficult to isolate experimentally because the effects of habitat loss are so great, they tend to mask the influence of fragmentation *per se*. Why then, separate the terms and create a debate over semantics? The differentiation between habitat loss and habitat fragmentation has important implications for conservation (Fahrig, 1997). Habitat loss has a significant impact on biodiversity independent of the effects of habitat fragmentation (Fahrig, 2003). Empirical evidence suggests that the effects of fragmentation on biodiversity loss are much weaker than the effects of habitat loss (e.g. Arroyo-Rodriquez and Dias, 2010), and that the former may even produce a positive effect (reviewed in Fahrig, 2003; Atkinson and Shorrocks, 1981; Chesson, 1985; Laurance et al., 2001; Bowman et al., 2002; Grez et al., 2004). The environmental heterogeneity that results from the changing properties of the landscape is an important factor in controlling biodiversity (Huston, 1994, 1999) that may contribute to the varying responses (positive or negative) of species to habitat fragmentation. For example, many species require more than one type of habitat for different life

stages or events and would consequently benefit from a heterogeneous landscape (Law and Dickman, 1998). If it is habitat loss rather than fragmentation *per se* (i.e. the breaking apart of habitat independent of habitat loss) that promotes species extinctions, then our focus should be only on restoration and not the spatial configuration of habitat across the landscape (Fahrig, 1997). If this is the case, then the concept of fragmentation appears to be used more as an intellectual attractor to incite a sense of urgency rather than as a valid conservation concern (Villard, 2002). Further, perhaps the current concern with fragmentation is misguided—or more accurately stated poorly understood—in that we have not adequately tested for the true effects of this process by controlling for habitat loss over the full range of biodiversity in real landscapes. Effective conservation management requires the distinction between the effects of habitat area and configuration on the population and behavioral ecology of a range of organisms, and until this is accomplished, the importance and influence of distinct landscape characteristics will remain unknown (McGarigal and Cushman, 2002).

A disconnect between the ecological and primatological literature

A disconnect has emerged between ecological literature and primatological literature, specifically in the field of landscape/spatial ecology, despite a similar general focus towards understanding how anthropogenic modification affects ecological processes in order to implement effective adaptive conservation management. This is particularly distressing because a majority of threatened primate communities now exist in fragmented forest habitats (Cowlishaw and Dunbar, 2000; Ganzhorn et al., 2003; Marsh, 2003; Godfrey and Irwin, 2007). A review of the ecological fragmentation literature by Lenore Fahrig (2003) reveals that out of 100 papers reviewed, 17 were empirical studies that isolated the effects of habitat loss by experimental design or statistical methodology (e.g. McGarigal and McComb, 1995; Wolff et al., 1997; Collinge and Forman, 1998; Trzcinski et al., 1999; Villard et al., 1999). A majority of the studies focused on birds (McGarigal and

McComb, 1995; Meyer et al., 1998; Trzcinski et al., 1999; Villard et al., 1999), while others focused on insects (Collinge and Forman, 1998; Tscharntke et al., 2002; With et al., 2002) or small mammals (Wolff et al., 1997). No medium- or large-sized mammals were part of an experimental design discussed in this review. There was no mention or cited reference of primates in the review as a whole.

In 2007, I conducted a keyword search in the Web of Science Database and PrimateLit using "primate and forest fragment" and "primate and forest fragmentation" which resulted in 50 articles. I also reviewed the series of papers in the book, Primates in Fragments, edited by Laura Marsh (2003) (see appendix). I recorded the taxa, study area, use of the term fragmentation, response variable being measured, and if a positive or negative effect was evident. The outcome of this review revealed that methodology used to identify the influence of landscape configuration and composition, in addition to local habitat structural attributes on species or community viability is poorly developed for non-human primates in fragmented forests.

Concept of fragmentation for primates

The review of papers concerned with fragmentation in the primatological literature was difficult because there was no clear distinction between habitat loss and habitat fragmentation. These terms were used synonymously without a clear definition provided by the authors of the process of fragmentation in the context of their research. As a result, there seems to be no consensus in how fragmentation is used, creating a challenge to quantify specific trends or measures of the use of the term fragmentation.

The following two examples illustrate the vagueness of the use of the term fragmentation. The first example demonstrates the interchangeable use of fragmentation and habitat loss. In a study conducted on silvery marmosets (*Mico argentatus*) in the Brazilian state of Pará (Goncalves et al., 2003), a sentence in the methods section states, "Fieldwork was carried out at four sites,

representing different degrees of habitat fragmentation" (p. 18). If one continues to read the methods section, it reveals that this study was focusing on four different forest fragments that varied in size (30 ha to continuous forest). I argue that this study was one focusing on the effects of habitat loss and not fragmentation *per se*. If it were a fragmentation study, as I have defined in this chapter, the above statement would have been referring to varying degrees of patch size and configuration and not solely to patches of different sizes. A second example is drawn from the introductory chapter of Primates in Fragments (Marsh, 2003). The following illustration (Fig 1.2) represents different "types" of fragmentation. Type "a" is described as regressive fragmentation and type 'b' is described as enveloping fragmentation. I would argue that these two types are actually habitat loss and not habitat fragmentation. The total amount of habitat is reduced in area, consistent with the definition of habitat loss, and there is no evidence of the habitat breaking into progressively isolated smaller patches of habitat consistent with habitat fragmentation *per se*. This book is the most recent compilation of papers concerning primate fragmentation research and is widely cited. The fact that fragmentation is incorrectly represented in the introductory chapter is of major concern and brings into question the focus of much *fragmentation* or more accurately stated, *habitat loss* primate research.

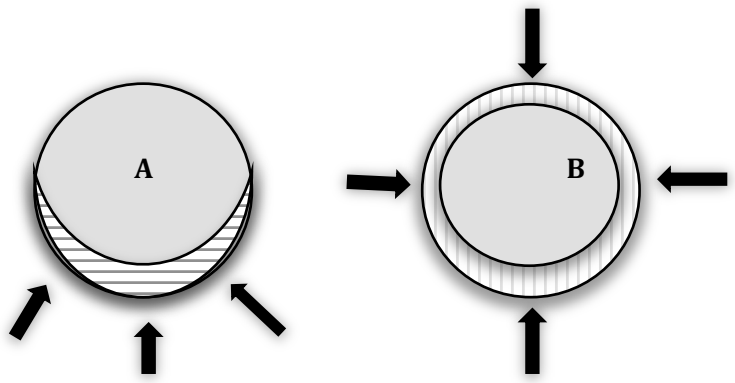

Figure. 1.2 Illustration of different types of forest fragmentation, modified from *Primates in Fragments* (Marsh, 2003:5).

I argue that the concept of fragmentation is non-specific and is used more as an overarching iniquity to incite conservation concern that encompasses several processes including habitat loss, but also variables such as disease (Gillespie and Chapman, 2006) and even the bushmeat trade (Wong and Sicotte, 2006). The literature on primates in fragments is quite extensive with researchers focusing on a variety of topics including: patch quality (Arroyo-Rodriguiz and Mandujano, 2006; Wong and Sicotte, 2006; Wong et al., 2006; Anzures-Dadda and Manson, 2007; Pyritz et al., 2010), species/patch characteristics (Estrada and Coates-Estrada, 1996; Tutin et al., 1997; Tutin, 1999; Onderdonk and Chapman, 2000; Mbora and Meikle, 2004; Wieczkowski, 2004; Galat-Luong and Galat, 2005; Worman and Chapman, 2006; Irwin, 2007; Zunino et al., 2007), population viability (Kinnaird and O'Brien, 1991), genetics (Craul et al., 2009), demography (Umapathy et al., 2011), parasites (Chapman et al., 2006; Gillespie and Chapman, 2006), seasonality (Chaves et al., 2011), edge effects (Lehman et al., 2006a,b), indirect effects (Estrada et al., 1999; Feeley and Terborgh, 2006), forest regeneration (Ganzhorn et al., 1999) and more recently the matrix/landscape (Anderson et al., 2007; Bodin and Norberg, 2007; Arroyo-Rodriguez and Mandujano, 2009). However, the majority of studies emphasize the importance of *patch size* (Table 1.1) in determining abundance (Chiarello and Melo, 2001; Estrada et al., 2002; Bicca-Marques, 2003; Chiarello, 2003; Baranga, 2004; Rodriguez-Toledo, 2004; Michalski and Peres, 2005; Wahungu et al., 2005; Wong and Sicotte, 2006; Cristobal-Azkarate and Arroyo-Rodriguez, 2007).

Patch size is an ambiguous measure of fragmentation and is indicative of studying habitat amount, not the process of fragmentation *per se* (Fahrig, 2003). This suggests that it is habitat loss that researchers are focusing on and not fragmentation *per se.* For example, Anzures-Dadda and Manson (2007) report that howler monkey (*Alouatta palliata*) distribution and abundance in northern Chiapas, Mexico corresponds with fragment area and canopy height that consequently affects the size of howler monkey populations. Further, Arroyo-Rodriguez and Mandujano (2006)

Table 1.1 Various topics of primate fragmentation research with an emphasis on patch size from a review of the literature in 2007.

Patch Quality	Distribution and Status	Patch Size	Species/Patch Characteristics
Anzures-Dadda and Manson (2007) Arroyo-Rodriguiz and Mandujano (2006) Marsh and Loiselle (2003) Wong et al. (2006)	Vargas et al. (2006) Huang et al. (2002) Dinesen et al. (2001)	Estrada et al. (2002) Chiarello and Melo (2001) Michalski and Peres (2005) Mendes- Pontes et al. (2007) Goncalves et al. (2003) Baranga (2004) Wahungu et al. (2005) Rodriguez-Toledo (2004) Wong and Sicotte (2006) Medley (1993) Chiarello (2003) Cristobal Azkarate and Arroyo-Rodriguez (2007) Bicca-Marques (2003) Ferrari et al. (2003) Gilbert (2003) Umapathy and Kumar (2003) Gonzalez-Solis et al. (2000)	Onderdonk & Chapman (2000) Wieczkowski (2004) Irwin (2007) Mbora and Meikle (2004) Tutin et al. (1997) Galat-Luong & Galat (2005) Zunino et al (2007) Estrada & Coates-Estrada (1996) Wieczkowski (2006) Worman and Chapman (2006) Tutin (1999) Schwarzkopf & Rylands (1989) Ukizitambara et al. (2007)
Parasites	**Edge Effects**	**Matrix/Landscape**	**Indirect Effects**
Gillespie and Chapman (2006) Chapman et al. (2006)	Lehman et al. (2006) Lehman et al. (2006) Norconk and Grafton (2003)	Anderson et al. (2007) Orjan and Norberg (2007)	Feeley and Terborgh (2006) Estrada et al. (1999)

found that fragment size was the variable that best explained differences in vegetation composition and structure and thus primate (*A. palliata*) abundance in Los Tuxtlas, Mexico. This study suggests that it is not fragmentation *per se* that affects howler monkeys but the loss of habitat that affects the habitat quality and in turn affects howler survival. Moreover, Bicca-Marques (2003) conducted a cross-study comparison asking, "How do howler monkeys cope with habitat fragmentation" (p. 283), but used forest size as the main predictor of home range size and habitat quality. A further example is illustrated by a study focusing on population size and density of *Colobus vellerosus*, ursine colobus, at the Boabeng-Fiema Monkey Sanctuary, Ghana (Wong and Sicotte, 2006). One of the main objectives of this research was to determine whether a relationship existed between population density and fragment size and isolation distance from the sanctuary. Again, research is claiming to focus on the effects of fragmentation but is actually evaluating the effects of habitat loss.

Harcourt and Doherty (2005) conducted a meta-analysis on "the first, comprehensive, quantitative global review of the consequences of fragmentation for primate species richness" (p. 631). The focus of this analysis was to quantify the general species-area relationship of 136 fragments at 33 study sites. The results indicate that primate richness and proportional richness decline linearly with fragment size in the spatial scales the researchers used including global, continent, and site. The authors provide conservation applications directed mainly toward primates that inhabit fragments of a certain size where long-term persistence of some species in the future is questionable and therefore more effective efforts should focus on larger-sized fragments. However, the authors do not discuss what constitutes a fragment to a primate. Some primates may use several small fragments across the landscape to acquire the resources needed for survival. It may be more appropriate to consider a collection of fragmens as one larger fragment. This suggests that these smaller fragments can actually be quite important for some primates and require consideration before they are dismissed as being unimportant in conservation initiatives.

As these examples demonstrate, the negative effects of small patch size and the increased isolation of habitat patches frequently are interpreted as fragmentation effects when they may be more accurately interpreted as the negative effects of large-scale habitat loss (Fahrig, 1997). This is not to say that habitat loss is insignificant. Indeed, primate research that focuses on loss of habitat demonstrates the detrimental impact of such a process (e.g. Laidlaw, 2000; Martins and Setz, 2000; Srivastava et al., 2001). Perhaps *fragmentation* should be regarded as a specific form of habitat degradation (Harrison and Bruna, 1999) rather than as an all-encompassing force.

The relationship of species-richness and persistence in forest fragments correlated with patch size and isolation, echoes the equilibrium theory of island biogeography that predicts smaller and more isolated islands support fewer species (MacArthur and Wilson, 1967). The extension of this insular theory to an analogy of "fragments as islands" suggests that a stark contrast exists between fragments and their uniform surroundings. Area is a poor indicator of extinction risk as the habitat used by different species amalgamates in more than just two dimensions (Haila, 2002; Heywood and Stuart, 1992; Whitmore, 1997). Yet, the island biogeography perspective still pervades conservation research in evaluating extinction risk (Haila, 2002). A landscape/spatial approach recognizes non-equilibrium, ecological heterogeneity moving away from a uniform Cartesian space (Haila, 2002). Moreover, the influence of habitat disturbance may have effects beyond patch size and isolation at the population and community level (Chiarello, 2003). Estrada et al. (2002) found that the mean troop size of black howlers (*A. pigra*) in Palenque, Chiapas, Mexico, was smaller in forest fragments compared to continuous forest. Twenty-two of the 44 fragments surveyed in this study contained populations of howler monkeys. However, without knowledge of the historical context of the current landscape, it is difficult to suggest why this is. It is rash and vague to conclude that the howlers have disappeared because of fragmentation when it could be a number of complex biological phenomenon simultaneously occurring. Is the discrepancy due to a lack of resources, hunting, the inability of howlers to reach particular fragments, a stochastic severe

climatic event, or maybe it is a historic accident that resulted in the howlers only being in certain areas of the forest when other forest areas were cut down. Further, in a comparison between 14 different sites in the Atlantic forests of Brazil, Chiarello compared data from northern Espirito Santo, southeastern Brazil (Chiarello and Melo, 2001) and the Plateau Range of western Sao Paulo state, southeastern Brazil (Cullen, 1997) mainly focused on the role of fragment size and hunting pressure in primate communities. Chiarello (2003) found no relationship between primate abundance and the size of fragments in the comparison between different sites. However, while focusing only on primate abundance in the forest fragments of Espirito Santo, southeastern Brazil, Chiarello and Melo (2001) did find a trend for higher densities in larger-sized fragments than in smaller ones. This could be explained by intrinsic and extrinsic factors involved in determining primate abundance beyond the mere size of the forest or the degree of isolation. Again, it is important to consider the disturbance history of the area, the heterogeneous characteristics of the landscape matrix, the biological idiosyncrasies of the organisms under study, and the spatial and temporal specificity of ecological processes (Chiarello, 2003).

In sum, these examples demonstrate a focus on habitat loss despite the intended focus on fragmentation. This suggests that since the focus of much primate research has actually been on habitat loss and not fragmentation *per se,* then the effects of different spatial configurations of habitat across the landscape and its effects on primate species persistence remain largely unspecified. The merger of conventional forest fragmentation research with the discipline of landscape ecology is highly applicable given the need for the greater understanding of landscape composition, configuration, and heterogeneity and their effects on ecological processes in the study of non-human primates.

When I developed this project in 2007, the literature that assessed the effects of fragmentation on primates was inconsistent in that the definition of the word fragmentation was used to mean different things and was measured in various ways. The word fragmentation also

was over-used in a manner consistent with inciting concern rather than reporting straightforward important results of the data. Instead of reserving "fragmentation" for a specific type of habitat degradation it was used to encompass all threats faced by primates due to habitat loss. An updated analysis of the primatological literature in 2012 demonstrates a continued focus on the "effects of fragmentation." Many authors still use fragmentation in the title of the paper or throughout the text in a way similar to studies from the earlier component of this review (e.g. Craul et al., 2009; Chagas and Ferrari, 2010; Pyritz et al., 2010; Schwitzer et al., 2011; Umapathy et al., 2011). An exception to this is a paper written by Arroyo-Rodriguez and Mandujano (2009) stating a very similar argument as that made in this dissertation. The authors assert that the definition and quantification of fragmentation is variable between primate studies, making the results difficult to interpret. The authors also stress the importance of understanding habitat requirements from the primate's perspective nested in a landscape ecology framework.

Landscape ecology

The concept of habitat fragmentation in ecological theory was first articulated by MacArthur and Wilson (1967:3-4) in the introductory chapter of The Theory of Island Biogeography:

> Insularity is moreover a universal feature of biogeography. Many of the principles graphically displayed in the Galapagos Islands and other remote archipelagos apply in lesser or greater degree to all natural habitats. Consider, for example, the insular nature of streams, caves, gallery forests, tide pools, taiga as it breaks up in tundra, and tundra as it breaks up into taiga. The same principles apply, and will apply to an accelerating extant in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization, a process graphically illustrated by Curtis' maps of the changing woodland of Wisconsin…

When fragmentation research began in the 1970s it was resolutely attached to the metaphoric analogy that fragments were equivalent to oceanic islands surrounded by a sea of

inhospitable land (Wiens, 1995a). Further, the application of island biogeography to landscapes manifested the idea that species impoverishment observed on small, distant oceanic islands is analogous to species numbers found in human-modified landscapes (Haila, 2002). A species-area pattern dominated the theory of researchers where small forest patches were equated with insolvency and extinction (Haila, 2002). Moreover, forest fragments were depicted as islands embedded in a spatially homogeneous landscape where a strict contrast existed between the fragment and the surrounding matrix. As a consequence, understanding how landscape variation affects ecological communities was largely ignored (Simberloff, 1997; Haila, 2002). The schematic representation of fragmentation that had developed was challenged based on theoretical and empirical ecological advances. Ecosystem equilibrium assumptions and closed communities were eventually rejected in ecology and the importance of scale was emphasized (Wiens, 1981; Delcourt et al., 1983; Wiens, 1984). Because different organisms may experience the same landscape in very different ways (Lindenmayer et al., 2008), the relevant features of a landscape might best be defined from an organismal perspective (Haila, 1990; Lord and Norton, 1990; Lima and Zollner, 1996). Landscape ecology emerged as a response to the new ecological developments:

> A uniform Cartesian space was replaced with environmental heterogeneity; equilibrium assumptions were replaced with spatial and temporal variability driven by non-equilibrium processes in various scales; and an unquestioned search for universal regularities was replaced with the acknowledgement of spatial and temporal specificity of ecological processes. (Haila, 2002:329)

As described by Turner (2005), Carl Troll, a German biogeographer, first defined landscape ecology in 1950 (Troll, 1950) that emerged from the European traditions of regional geography and vegetation science. But it was not until the 1980s that North American and Australian landscape ecology developed with an explicit focus on understanding the relationship between spatial heterogeneity and ecological processes (Pickett and Cadenasso, 1995; Turner, 1989; Turner, 2005). Specifically, landscape ecology aims to understand the effects of spatial pattern (composition and

configuration) on process, and thus landscape ecology accounts for relevant spatial scale defined by the organism (Turner, 2005). Moreover, landscape ecology extends beyond the single "patch" and addresses the entire landscape including elements of the matrix, the complex area between forest patches. This is a highly useful exemplar particularly when focusing on movement patterns, dispersal, and habitat use in the context of a larger, dynamic landscape mosaic. Furthermore, because changes in land use alter landscape composition and configuration, landscape ecology and biological conservation are certainly linked.

Consequently, as previously stated, the effects of habitat loss and fragmentation have received much attention (e.g. Saunders et al., 1991; Andren, 1994; Haila, 2002; Fahrig, 2003). As such, a landscape ecology perspective is well integrated with ecological research (Turner, 2005). Yet prevalent in studies of small mammals (Wolff et al., 1997; Stapp and Van Horne, 1997; Bakkar and Van Vuren, 2004; Gorresen and Willig, 2004), birds (Aberg et al., 1995; Belisle et al., 2001; Stouffer et al., 2006; Manning et al., 2007;), amphibians (Joly et al., 2001; Lowe et al., 2006) and insects (Condrat et al., 2000; Jonson et al., 2001; Goodwin and Fahrig, 2002; Driscoll and Weir, 2005; Benedick et al., 2006; Winfree et al., 2007), this is an approach that has yet to find its way to non-human primate studies (but see Anderson et al., 2007; Anzures-Dadda and Manson, 2007). In one of the few research projects with a landscape ecology focus, Anderson et al. (2007) evaluated the use of a heterogeneous landscape in southern Kenya by the Angola black-and-white colobus (*Colobus angolensis palliatus*). The results specify that the use of the matrix between forest fragments by the colobus was related to the amount of both vegetation greater than six meters and to food tree cover indicating the importance of using a landscape level approach to habitat management. The lack of primate research focusing on spatial/landscape ecology demonstrates the disciplinary divide.[3]

[3] The Stability of Altered Forest Ecosystems Project (SAFE Project) has recently been developed (Ewers et al, 2011) in Malaysian Borneo that has arisen due to opportunity from palm oil plantation expansion. This long-term scientific experiment was generated to address questions

Central to my argument is that the focus of much primate research has been on habitat loss and not fragmentation and spatial heterogeneity *per se*. As a result, different spatial configurations of habitat across the landscape and its effects on primate species persistence remain unspecified. The union of primatology with the discipline of landscape ecology is necessary given the need for a greater understanding of landscape structure and pattern and its effects on ecological process in the study of non-human primates. Effective conservation management requires a distinction between the effects of habitat area and configuration on the population and behavioral ecology of a range of organisms. The influence of distinct landscape characteristics and quantifying the heterogeneity pattern of the landscape are important components to ultimately understanding process and habitat use by biota (Fahrig, 2003).

A powerful application of landscape ecology to gain a greater understanding of forest fragment biology lies within its maps, images, spatial statistics, and ecological modeling. Geographic information systems (GIS) is an effective tool for integrating information and depicting both real and synthetic landscape patterns (Wiens, 2002). Moreover, GIS is an authoritative conservation tool evidenced by the speed and accuracy of GPS/GIS technology and ability to address important empirical and theoretical conservation issues. GIS enables the acquisition, storage, analysis, and display of vegetation mapping and ecological spatial data of different environments. GIS applications are valuable in illustrating the spatial and altitudinal distribution of biodiversity, differential habitat use by individuals and populations, and subsequent identification of conservation priority hotspots (e.g. Campbell, 1994; Smith et al., 1997; Miller et al., 2004; Irwin et al., 2005; Bergi et al., 2007). The production of a visual map facilitates the generation of patterns from complex landscape data and is important in providing conservation authorities with up to date information on critical habitat use by biodiversity and local communities.

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pertaining to the effects of forest fragmentation and deforestation on biodiversity. This project will incorporate research focused on a variety of plants and animals including large-bodied mammals and primates.

As noted above, landscape ecology is the study of how landscape structure affects the abundance and distribution of organisms (Fahrig, 2005), and with biodiversity hotspots (*sensu* Myers et al., 2000) rapidly shrinking in area, synergistic spatial analyses are essential to understanding spatiotemporal relationships between any species and its environment. Wiens (2002:17) notes that E.O. Wilson (2000) suggested that landscape ecology "is about to emerge as one of the most significant intellectual frontiers of the twenty-first century."

Habitat quality

An important area of current landscape ecology research is aimed at disentangling the effects of landscape composition (what and how much is there) and landscape configurations (how is it spatially arranged) on populations (Fahrig, 1997; McGarigal and Cushman, 2002). Quantifying habitat attributes and the landscape pattern of a forest fragment is therefore essential before an understanding of a particular species' or community's response can be reached. The concepts of habitat quality and environmental heterogeneity however, are poorly defined in forest fragment studies involving primates. A qualitative binary definition of primary versus degraded or secondary forest is the principal research focus. This allows for only a narrow assessment of the magnitude of variation in between (Lindenmayer et al., 2008). The quality of habitat will influence survival, reproduction, dispersal, and successful locomotion for an organism. The concept of habitat quality has clear value; however, operationally it is difficult to define and implement (Wiens, 2002). This stems from different perceptions of the environment: the individual organism's and the researcher's. The environment may be perceived as unsuitable habitat to the researcher, but the organism may focus on the structural integrity of the habitat regardless of the broad generalizations of "primary" versus "secondary" or "degraded" forest made by the researcher. Quantifying the environment is more informative than qualitative categories. Furthermore, secondary forests or degraded habitat constituted approximately 17% of clear-cut

tropical land cover in the 1990s and will likely dominate tropical forest landscapes in the future (Wright, 2005; Wright and Muller-Landau, 2006). Yet, this landscape feature is often excluded from forest assessments to implement conservation planning (Brown and Lugo, 1990). The varying structural conditions of secondary forest are important in retaining significant amounts of biodiversity (Cadotte et al., 2002) and their spatial adjacency or isolation will determine accessible habitat and thus primate utilization and mobility.

Broad categories oversimplify the nuances of vegetation structure and composition and critical resources found to increase individual fitness. There is an urgent-benign continuum on which primates respond to broad-scale habitat modifications where inter- and intra-specific differences vary. We do not fully understand the limits of flexibility concerning primate ecological aspects nor demography that allow the persistence of some primate taxa over that of others in a fragmented landscape (Ehardt et al., 2005). To be able to identify which characteristics of a species are more sensitive to the effects of fragmentation would be useful in providing management plans (Turner and Corlett, 1996; Davies et al., 2000; Onderdonk and Chapman, 2000; Henle et al., 2004; Viveiros de Castro and Fernandez, 2004; Ehardt et al., 2005). Vulnerability greatly varies between taxa making multiple models for every species a seemingly difficult task that requires an expansive time frame. Because of this, projections have been made for a population and its ability to persist in a fragment based on determined characteristics which appear to repeatedly influence survival or local extinction [(Davies et al., 2000; Jonsson and Ebenman, 2001; Ganzhorn et al., 2003; Henle et al., 2004; e.g. populations that are small, fluctuate drastically due to 'environmental vagaries', have low intrinsic growth rates, maintain a high degree of arboreality, require large home ranges, have a specialized diet, and possess moderate dispersal power including an inability to use the matrix (Bierregaard et al., 1992; Fagan et al., 1999; Henle et al., 2004; Mbora and Meikle, 2004)].

Defining habitat quality from the individual organisms' defined perceptive scale is an additional essential component needed in our understanding of the persistence of some primate

taxa over that of others in fragmented landscapes. Species persistence patterns and population viability in modified, heterogeneous forests depend on a detailed assessment of forest structure and the quantification of spatial heterogeneity (Haila et al., 1989, 1996; Niemela et al., 1996; Turner, 2005). This sophisticated type of analysis will allow meaningful statements regarding variation in patch quality and why organisms occur where they do or move as they do in a landscape. Multivariate habitat heterogeneity at multiple scales imposes variable responses from different organisms. Identifying key factors that explain variation in the presence or absence of different organisms is a primary goal in landscape ecology (Turner, 2005) and when extended to primate conservation research may provide valuable insight into population survival. Moreover, a multivariate approach allows for the departure from single-species studies, as there is a need to address community dynamics in heterogeneous landscapes (Opdam et al., 2003; Turner, 2005).

A primate community focus in fragments is rare (Cowlishaw and Dunbar, 2000). Although, there is a growing consensus that community-focused conservation efforts considering multiple habitat requirements are more effective and proactive than a single species approach (Franklin, 1993; Noss et al., 1997; Fleagle et al., 1999; Freudenberger and Brooker, 2004; Roberge and Angelstem, 2004; Whiteley et al., 2006). Results from community ecology research are informative and shed light on ecosystem complexity. A long-term primate community (*Pan troglodytes, Cercocebus albigena, Colobus satanas, Cercopithecus nictitans, Cercocebus pogonias*) research project in a forest fragment in the northern section of Lope Reserve, Gabon revealed that population density of the fragment was twenty-three times higher than the density in the continuous forest (Tutin, 1999). The different species of primates were able to relax inter-specific feeding competition through behavioral adaptations, demonstrating the importance of an interacting community. Research conducted in Lago Uauacu, Brazilian Amazonia demonstrated the importance of habitat heterogeneity in determining platyrrhine diversity, abundance and biomass. Differences in floristic composition, habitat structure, and soil fertility indicated differences in the primate

community (*Saguinus mystax* ssp., *Saimiri* cf. *ustus, Aotus* cf. *nigriceps, Callicebus cupreus, Callicebus torquatus purinus, Pithecia albicans, Cebus albifrons versicolor, Cebus apella, Alouatta seniculus seniculus, Lagothrix lagotrichacana, Ateles chamek, Cebuella pygmaea*) found between terra firme, varzea, and iagapo forests analyzed (Peres, 1993). Detailed knowledge of species movement patterns and substrate use within a community context is crucial to understanding the importance of differential landscape mosaics and configuration.

The consideration of multiple species highlights the importance of an organism-focused view of heterogeneity because the same landscape may look very different to different species (Wiens, 1989). Furthermore, connectivity, "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993), is an important component in animal movement and has to be defined from the perspective of the species or process of interest (Lima and Zollner, 1996). Landscape context is also important (Mazerolle and Villard, 1999; Turner, 2005). Local habitat quality may be assessed by an organism in part as a function of what habitat quality is adjacent to a given habitat patch (e.g. Lindenmayer et al., 1999; Steffan-Dewenter et al., 2002). So, it is not only important to quantify *what* a patch is (e.g. composition, boundary length and shape) but also *where* it is in terms of neighboring ecological properties that filter certain organisms:

> It is the relationships among landscape elements as much as their variety that make landscapes important, for these relationships can affect the interactions among elements in a mosaic as well as what goes on within individual patches. (Wiens, 2002:4)

The mobility of a species and the pattern of the habitat will influence the perceived connectivity of the landscape (Vos et al., 2001; Freemark et al., 2002; Goodwin and Fahrig, 2002). This will depend on the particular habitat preferences of the species and the ability or willingness to traverse gaps of unsuitable habitat (Lima and Zollner, 1996). For example, in Lope Forest, Gabon Tutin (1999) indicates that it is important to consider fundamental ecological differences between

primate populations that reside in a fragment versus primates that visit depending on temporal food supplies. Resident guenon populations need to find food resources to meet their needs every day of the year. In contrast, chimpanzees are capable of moving between fragments and the continuous forest and can take advantage of temporally abundant food resources. When the resources are depleted, the mobile primates can then search out new food resources in another forest patch. An emphasis on habitat heterogeneity and landscape heterogeneity are therefore important.

Heterogeneity

"The quantification of spatial heterogeneity is necessary to elucidate relationships between ecological processes and spatial patterns; thus the measurement, analysis, and interpretation of spatial processes is important in landscape ecology" (Turner, 2005:323). The environmental heterogeneity that results from the changing properties of the landscape is a significant factor in controlling the continued survival of biodiversity (Huston, 1994, 1999) that may contribute to the varying responses (positive or negative) of different species. Many species require more than one type of habitat for different life stages or events and would consequently benefit from a heterogeneous landscape (Law and Dickman, 1998). For example, in the Amazonian rain forests, Schwarzkopf and Rylands (1989) documented that primate species richness increased in heterogeneous environments. Despite being a small fragment (10 ha), this forest supported three primate species (*Alouatta seniculus, Saguinus midas, and Pithecia pithecia*) in part due to the habitat structural diversity (Schwarzkopf and Rylands, 1989). In addition to the fragmented forest of Manaus, Brazil (Schwarzkopf and Rylands, 1989), a positive association between species richness and heterogeneity has also been identified in an undisturbed western forest of Madagascar (Ganzhorn, 1994) and logged forest in Kibale, Uganda (Skorupa, 1986). Knowledge of this multiple habitat use is important for practical conservation management (Law and Dickman, 1998).

Furthermore, beyond assessing habitat use, documenting specific habitat structural variables (e.g. sleeping tree or a tree located in a prime location to promote mobility from one area in the forest to another) that support primate species is critical to informing reforestation projects. For example, conservation biologists advocate corridor projects that increase connectivity between habitat patches in order to maintain re-colonization and gene flow to ultimately prevent local extinctions (Franklin, 1993; Meffe and Carroll, 1994; Rosenberg et al., 1997). However, extensive corridor projects connecting forests are difficult and require many complementary variables (i.e. animal use, successful forest re-growth, monetary resources, and time). A more immediate approach to increase connectivity, movement, and even basic survival is to identify key structural variables important to the sustainability of primate communities. Specifically, by defining the variation in habitat structural variables, the factors that best explain primate community assemblages in different habitat types can be assessed. For instance, Tutin (1999) identified three different dense liana tangles covering several trees that were important "safe places" used for resting by the guenon population in the fragment. It would be interesting to note other primate species that use these lianas and even biota beyond primates. Tutin's research being an exception, an emphasis in generalities dominates primate research in this subject matter. For instance, red colobus and crested mangabey numbers grow with an increase in area-to-perimeter ratio and canopy height (Medley, 1993). Other research has shown that tamarin persistence is associated with secondary growth around fragment perimeters (Rylands and Keuroghlian, 1988). Further, howler monkeys have been found more frequently in fragments with canopy heights greater than 10 meters (Rodriguez-Toledo et al., 2003). Indeed, these studies have provided important information in our quest to understand primate responses to fragmented living but the next step is twofold: to move beyond generalities and identify particular forest structural attributes that are vital, and to identify these structural variables not just for single species, but for entire primate communities. The appropriate temporal or spatial scale is not always obvious, especially when

focusing on complex ecosystems where different species may have different requirements for optimal survival. An important question to ask then is at what point does internal heterogeneity become fragmentation (Tews et al., 2004)?

Land management practices can then proceed so that certain critical trees or other forest attributes will not be removed and critical structural elements can also be reforested. For example, a certain species of tree utilized by the red colobus and crested mangabeys in the Tana River forests is also an important material for constructing canoes and collecting honey (Mbora and Miekle, 2004). Detailed empirical findings will be able to contribute to our understanding of which habitats or even single-tree species are primary keystone components (e.g. Terborgh, 1986) to the sustainability of the primate communities inside of forest fragments. Prior research has indicated the importance of feeding trees. For example, figs (*Ficus* spp.) are important keystone species for frugivorous primates (e.g. Leighton and Leighton, 1983; Terborgh, 1986). In addition to vital feeding trees, specific trees that facilitate movement through the environment are equally important keystone structures (Tews et al., 2004). The results will contribute valuable information to reforestation programs by identifying important vegetative structural attributes utilized in primate (and other fauna and flora) movement patterns as well as indicating priority areas to reforest.

Positive or negative response of primates to fragmentation

An important element in conservation research is the assessment of species' responses to habitat degradation to inform conservation priorities. A primary objective of this critical review of the literature, therefore, was to attempt to quantify if fragmentation *per se* prompted a positive or negative response from different primate species. However, because there is no separation of the terms fragmentation and habitat loss, it was difficult to accurately interpret if there is a positive or negative response from different primate species to fragmentation *per se*. It was not always clear

that it was in fact fragmentation causing the response and not habitat loss, or vice versa. Moreover, perhaps the response of individuals is not necessarily a dichotomous (loss or fragmentation) situation, but instead, is a result that involves different combinations of intrinsic factors compounded by extrinsic factors that fluctuate temporally and spatially operating differently on each individual. Further, habitat disturbance may affect population dynamics at different levels (e.g. sex ratios) and different taxa may respond to fragmentation at varied rates (Debinski and Holt, 2000) where some species may be persisting through time solely due to the longevity of a few individuals that are no longer reproducing (Saunders et al., 1991; Turner and Corlett, 1996). Because of this, the capacity to classify different species according to their vulnerability within forest fragments would be a valuable tool for assessing and implementing management plans (Davies et al., 2000; Jonsson and Ebenman, 2001; Chapman et al., 2005).

However, vulnerability greatly varies between taxa, making multiple models for every species a seemingly difficult task requiring an expansive time frame. Despite this difficult task, projections can be made for a population and its ability to persist in a fragment based on determined characteristics that appear to repeatedly influence survival or local extinction (Jonsson and Ebenman, 2001; Henle et al., 2004; Isaac et al., 2005). For example, populations that are sensitive to diminishing habitat and thus more prone to local extinction have particular characteristics. These population and individual traits include: being small and therefore subject to a loss of heterozygosity, having low intrinsic growth rates, maintaining a high degree of arboreality, being large-bodied and requiring large home ranges, having specialized diets with limited ecological flexibility, having slow individual life history characteristics (e.g. long interbirth intervals and juvenile period), feeling stress, and possessing moderate dispersal power, including an inability to use the matrix between habitat patches (Johns, 1987; Bierregaard et al., 1992; Strier, 1992; Fagan et al., 1999; Gonzalez-Solis et al., 2001; Henle et al., 2004; Isaac et al., 2005).

In addition, whatever the response, it may be more of a coping mechanism or behavioral adaptation to "cope" with the changing environment that is not easily designated as either positive or negative. Several examples illustrate this point. Results of a year-long study in Tsinjoarivo, eastern Madagascar on four groups of diademed sifakas (*Propithecus diadema diadema*) indicate that groups living in forest patches have less group cohesion than groups living in continuous forest (Irwin, 2007). The reduced group cohesion of the fragment groups is a result of the patchy distribution of food resources in the smaller forests (Irwin, 2007). This behavioral adaptation demonstrates more of a coping mechanism than evidence of a positive or negative response. A second example is illustrated by Temminck's red colobus (*Procolobus badius temmincki*) in the Fathala Forest, Saloum Delta National Park, Senegal (Galat-Luong and Galat, 2005). This population of red colobus has been studied for 30 years during which more than 50 percent of the forest has disappeared (Galat-Luong and Galat, 2005). However, despite the habitat loss, the red colobus population has not drastically declined, but instead has developed some interesting behavioral adaptations to cope with the changing environment. Some of these behaviors include: a greater consumption of fruits and new foods such as grasses and seeds despite their specialized folivore physiology, increased terrestrial locomotion despite arboreal skeletal morphology, and a new founded polyspecific association with green monkeys due to an increased threat from dog and hyena attacks as a result of terrestrial behaviors.

Increased terrestrial locomotion has been observed in other primate species as well when the forest is essentially gone, preventing arboreality. The golden-crowned sifaka (*Propithecus tattersalli*) "copes" in a fragmented landscape by bipedally jumping across more than 200 meters of savanna to reach a different forest fragment (Vargas et al., 2002). The mantled-howling monkey (*Alouatta palliata)* has also been observed traveling distances of 10 to 200 meters to reach different fragments (Estrada and Coates-Estrada, 1996) and brown capuchins (*Cebus apella)* are able to cross open pastures (Michalski and Peres, 2005). Although a straightforward positive or negative

response was not discernable among different primate species, it is evident that ecological and behavioral flexibility are important primate characteristics that prevent immediate extinction of populations faced with rapid environmental change.

The literature reviewed in this chapter suggest that habitat loss has impacted biodiversity far greater than fragmentation at this point, but again this is related to the lack of studies that do truly focus on fragmentation of the landscape. Fahrig (2003:505) found that "when fragmentation *per se* did have an effect, it was as likely to be positive as negative." Due to large variation in the conditions it was also difficult to discern what factors were contributing to the positive or negative responses to fragmentation *per se*. An important point Fahrig (2003:505) makes at this juncture is that the positive effects of fragmentation "can not be explained as merely responses by "weedy," habitat generalist species" (e.g. McGarigal and McComb, 1995; Tscharntke et al., 2002). This is an important conclusion to also consider when evaluating primate responses.

It is important to consider what is a negative effect and a positive effect of fragmentation *per se*. Fragmentation *per se* implies an increasing number of smaller forest patches that at some point will be too small to support any primate troop. This will be compounded by primates that cannot use the matrix and will therefore be confined to a large number of very small patches across the landscape. A second major negative effect of fragmentation *per se* is edge effects because fragmentation of the landscape will contain more edge for the amount of remaining habitat (Fahrig, 2003). For instance, an increased "edge" can result in more predation events by top trophic predators including humans. In these instances it is very difficult to separate out the negative effect of habitat loss because habitat loss is so detrimental.

As discussed earlier in this chapter, fragmentation emerged from island biogeography (Haila, 2002) where the concept of island size and isolation were extended from island archipelagos to terrestrial systems. This resulted in viewing isolation as habitat subdivision even though it is linked to habitat loss. Much discussion centers around the theory of island biogeography in

fragmentation research and less around a parallel research effort that emerged separately discussing the positive influence that fragmentation could have on biodiversity (Fahrig, 2003). For example, some experiments demonstrated that landscape subdivision can positively effect predator-prey systems by providing refugia (Huffaker, 1958). Theoretical studies also indicated that fragmentation enhances competition between two species (Levin, 1974; Slatkin, 1974). A benefit of fragment living for primates may manifest itself in the form of relaxed feeding competition from larger species when resources are scarce, behavioral flexibility to fission into smaller groups without worry of relocating the larger group, reduced travel costs, and monitoring the quantity and quality of food resources is diminished (Tutin, 1999). Habitat subdivision can also affect single species positively, decreasing the probability that an entire population will be extirpated by local disturbances (Roff, 1974; den Boer, 1981). The possibility that fragmentation *per se* could have a positive effect on biodiversity was largely ignored. More recently, Bowman et al. (2002) indicate that habitat fragmentation *per se* could result in a positive effect on population density because a larger number of patches would result in a higher immigration rate. Many species require more than one type of habitat (Law and Dickman, 1998), as previously discussed, and therefore would benefit from a heterogeneous landscape. For a given amount of habitat, a more fragmented landscape would contain a higher level of different types of habitat (Fahrig, 2003). A final possible positive effect of fragmentation is that some species do respond positively to edge effects (Chiarello, 1994; Crockett, 1998; Laurance et al., 2001; Lehman et al., 2006a).

In sum, habitat loss does have a negative effect on biodiversity. Indeed, tropical rainforests are disappearing faster than any other biome (Myers, 1991) - "the numbers are staggering and grotesque" (Marsh, 2003:1). However, the effects of the breaking apart of the landscape and consequent heterogeneity, independent of habitat loss has received little attention, is too small to detect, or actually has a positive effect on biodiviersity (Fahrig, 2003). This positive effect of fragmentation contrasts with theoretical initiatives (Hill and Caswell, 1999; With and King, 1999)

and directly has critical implications for conservation. If habitat loss is the major force driving negative impacts then we need to focus on restoration and habitat preservation. Perhaps the current concern with fragmentation is a misguided effort or just poorly understood in that we have not adequately tested for the true effects of this process by controlling for habitat loss over the full range of biodiversity, including primates, in real landscapes. And if research reveals that it is habitat loss that is negatively effecting a population, then we need to indicate this in the primatological literature and refrain from using buzzwords to incite concern. Article titles using "fragmentation" to indicate a broad spectrum of the effects of human activities is causing this single term to lose its usefulness (Fahrig, 2003).

This dissertation is fundamentally about exploring the relationship between structure and lemur community movement, but this type of information will undoubtedly be useful for addressing questions of primate extinction risk, as the role of landscape spatial patterns in primate extinctions have been relatively understudied in modern ecosystems.

CHAPTER 2
METHODOLOGY

Study Site and History

This research was conducted May-November, 2009[4] in Betampona Strict Nature Reserve, northeastern Madagascar. Betampona Strict Nature Reserve (BNR) is one of the last remaining tracts of eastern lowland rainforest (Green and Sussman, 1990), home to many endemic plant and animal species. The alarming rate of deforestation was recognized in the early 1990s (Green and Sussman, 1990), which has continued until the present day (Dulfis, 2003; Irwin et al., 2005; Harper et al., 2007). The amount of rainforest in Madagascar has decreased the most relative to other forest types, with 40% cleared between 1950 and 2000 (Harper et al., 2007). Moreover, in 2000 more than 45% of the remaining forest existed in <500 km^2 forest fragments (Harper et al., 2007), making disturbed forest the "norm". If the rate of forest loss continues at 150,000 hectares per year, then the primary vegetation of Madagascar will all be lost by the year 2067 (Moat and Smith, 2007). Evaluating the prospects of biodiversity that remain in these small isolated forests is central to conservation management in Madagascar (Irwin et al., 2010).

BNR was established in 1927 and in 1966 became the first of the strict nature reserves in Madagascar (Andriampianina and Peyrieras, 1972). This classification only allows the entrance of scientists with research permits and excludes tourism. The reserve is located between 17º15'-17º55'S and 49º12'-49º15'E, 40 kilometers north-west of Tamatave (Toamasina) on the eastern coast of Madagascar (Britt, 2000). Betampona is a forest that encompasses 2,228 hectares of steep undulating terrain with an altitude ranging from 275 to 650 meters above sea level (Razokiny, 1985). As one descends from the ridge tops to the valley floors, forest structure and composition varies (Britt et al., 2003a) with Moraceae, Lauraceae, Euphorbiaceae, Clusiaceae, Sapotaceae, Arecaceae, Myrtaceae, Liliaceae, Burseraceae, and Annonaceae being the most important plant

[4] The coup impacted my research by delaying the intial start date by several months.

families (Britt et al., 2003a). The ecology of BNR is threatened with anthropogenic pressures (e.g. slash and burn farming and invasive plant spread) that modify the landscape. As a result, 50% of the original 2,228 hectares of BNR exists as intact primary forest with the remaining forest in various stages of re-growth (Britt et al., 1999, 2003). The mountainous terrain in conjunction with invasive plant spread and re-growth has generated significant identifiable differences in habitat structure, configuration, and composition throughout the reserve (Mertz and Sandberg, personal observations). As such, the landscape of BNR is appropriate for investigating how environmental heterogeneity affects species diversity and community structure.

Approximately 50 years ago the forest of Betampona was continuous with Sahivo and Antanamalaza classified forests (Britt et al., 1999). Betampona is now an isolated forest (Britt et al., 2003b) saved from deforestation by its extreme undulating terrain. The Parc National/RNI de Zahamena, approximately 20 kilometers to the northwest, and the Reserve Speciale de Mangerivola, 30 kilometers to the southwest, are the two closest protected forests (Britt et al., 2003a). Of the original 2,228 hectares of Betampona, 50% remains intact primary rain forest (Britt et al., 1999, 2003a). Today, areas throughout the reserve are composed of non-primary forest and longoza thickets (*Afromomum angustifolium*) (Welch and Katz, 1992; Britt et al., 2003a). Non-primary forest areas also include traveller's palm (*Ravenala madagascariensis*), true palm species (*Pandanus*), and invasive species such as guava (*Psidium cattleianum*) (Welch and Katz, 1992; Britt et al., 2003a). This is the result of present day selective logging of precious hardwoods and historical agricultural encroachment.

A 100-meter Zone of Protection (ZOP) has been established around the perimeter of the reserve. This protected space is intended as a buffer between the eleven subsistence-farming dependent villages surrounding the reserve and the reserve edge proper on which the traditional slash-and-burn farming practice is not legally permitted. This land has historically been and continues to be cultivated by local villagers. Therefore a friendship with the local communities is

vital in maintaining the buffer and any future conservation endeavors in and around the reserve. The well-established NGO, Madagascar Fauna Group (MFG), worked collaboratively with local residents in creating a plan to reforest the ZOP. This collaboration was important so that the reforestation effort would meet the needs of the local people as well as the MFG. Both parties agreed that the MFG would provide commercial and native trees for planting in the ZOP as well as additional commercial trees for people's communal areas.

The rapid expansion of the human population surrounding BNR combined with elevated poverty levels has increased the demand for land and consequently has intensified the pressure on the forest. In the past, the forest suffered from small-scale illegal wood extraction and hunting. Both of these threats have recently intensified in light of the presidential coup and subsequent political instability. This instability was the result of international agencies that pulled aid and a decentralized government. The coup yielded a situation where there was dramatically reduced enforcement of law in many protected areas and parks throughout Madagascar. This instability created the ideal situation for criminals to take advantage of Madagascar's resources. The environmental pillage is primarily in the form of harvesting valuable hardwoods, including rosewood and ebonies. Timber is not the only commodity sought after; a commercial bushmeat market for lemurs has also emerged. Since the coup, BNR has also experienced increased levels of ecological pressure by armed bandits. Over the course of my study, nocturnal research was banned in the reserve because of safety issues. Felled trees and boards that have been cut for easier transport of the valuable Pallisandre tree have been found in the reserve. Numerous lemur traps constructed out of vines have also been found throughout BNR. The hunter often will cut a clearing in the vegetation such that the lemur will move along the strategically placed branches leading directly to the snare. The snares are often baited with fruits to make them more enticing. The hunting practice is for both local consumption and for trade.

Unfortunately the coup has increased the already high poverty levels of many people living

in villages surrounding BNR. Poverty forces people to engage in these ecologically destructive behaviors. There are few alternatives and people must be opportunistic to feed their families. Many people are worried about even having enough money to buy rice, their staple food. The coup and consequent instability demonstrates the multifaceted nature of conservation endeavors and how even the best of intentions, long-standing relationships, and trust can disintegrate when faced with hardship and opportunity. However, the MFG's close involvement with people living outside BNR through the reforestation project and the Saturday school programs may have thwarted more intense destruction within the reserve.

Furthermore, Madagascar National Parks (formerly ANGAP) have stated that they are interested in changing the status of Betampona from a Reserve Intégrale to a Reserve Spéciale or even a National Park in their effort to become more financially sustainable. This change in reserve status would cause an influx of people and impact on the forest. While there are economic benefits to this, the MFG wants to assure that it is done in as sensitive a manner as possible to avoid damage to the most threatened habitats and species within Betampona (Freeman, personal communication). For this to be a successful endeavor and for the development of a practical plan that will allow access to the public while still protecting the most vulnerable areas in the reserve, the MFG needs data sets such as mine, to make informed decisions.

Betampona Biodiversity

At least 88 species of bird and 70 amphibian species inhabit BNR's forest along with 67 species of reptile, including the critically endangered gecko *Paroedura masobe* and the prehistoric looking leaf-tailed gecko (*Uroplatus* sp.). The reserve is also home to countless plant and invertebrate species – many of which have yet to be described. Eleven primate taxa are currently found in BNR including five diurnal and six nocturnal species: *Propithecus diadema diadema* (diademed sifaka), *Indri indri* (indri), *Varecia variegata* (black and white ruffed lemur), *Eulemur*

fulvus albifrons (white fronted brown lemur), *Hapalemur griseus griseus* (bamboo lemur), *Microcebus rufus* (bamboo lemur), *Cheirogaleus major* (fat-tailed dwarf lemur), *Phaner furcifer furcifer* (fork-marked lemur), *Lepilemur mustelinus* (sportive lemur), *Avahi laniger laniger* (woolly lemur), and *Daubentonia madagascariensis* (aye-aye) (Welch and Katz, 1992; CBSG, 2002). Of these 11 taxa, two (*Indri indri* and *Propithecus diadema diadema*) are classified as Endangered and one, *Varecia variegata,* Critically Endangered (IUCN, 2011). The landscape of BNR combined with the remarkable number of species found there makes BNR an ideal ecosystem for the development of a landscape model that illustrates how different spatial patterns affect species diversity and community structure.

Temperature and rainfall

Rain can be expected for more than 300 days each year with over 2000 mm falling annually. The average annual temperature is 75.2°F with annual lows of around 60.8°F between June and August and annual highs of 89.6°F possible between December and February. Temperature was recorded via a digital thermometer placed approximately 1600 meters inside the forest. A palm-roofed shelter has been constructed to house the thermometer and protect it from the elements. Adjacent to the shelter is a mounted plastic column marked in millimeter increments and used to collect rainfall. Both temperature and rainfall measurements were collected on a daily basis. In 2009 rainfall varied per month with the lowest amount falling in June (4.1 mm) and April experiencing the most (26.9 mm). The maximum temperatures were in January with a high of 87.1°F and low of 71.2°F. Minimum temperatures were experienced in July with a high of 69.1°F and low of 60.6°F. Humidity was fairly constant ranging from a high of 96.6% to low of 81.1%.

Research Methodology

***Vegetation Analysis*:** A detailed assessment of the structural variation within BNR was necessary for the development of a spatial framework within which to work. Sixty-one vegetation plots were

previously quantified in BNR as part of my preliminary research. These plots represent different microhabitat structural types of BNR. The purpose of establishing multiple plots in different locations in the reserve was to quantitatively represent the heterogeneity of BNR to test for the effects of landscape composition and configuration on lemur occurrence. From this preliminary analysis, 8 of these plot locations were used and expanded upon in this research. Four 10 m x 10 m plots were placed within a 50 m radius at each of the 8 plot locations. These quantified plots collectively represent a patch, a central component of this research. A patch is defined here as a relatively homogeneous (e.g. similar in structure) area that differs from its surroundings. The first plot was placed approximately at the location of the previous plot established during my preliminary research. The center of the next plot was located at a random compass direction and fixed distance of 30 m. The last two plots were positioned 120 degrees from the first (following Ralph et al., 1993). At each plot, the number of new trees and herbaceous shrubs (0.15 m, 1.2 m, 1.8 m) were counted within a 1 m^2 block. This was repeated in 4 different locations in the plot. Tree composition and the number of each type of tree were recorded for each 10 m x 10 m plot. The Malagasy name for the trees that could be identified was recorded and then later translated into their genus and species designations. The local Malagasy guides that live on the periphery of BNR have an intimate knowledge of the forest and the vegetation. Previous research in BNR has established the consistency of Malagasy names to certain taxa of plants and the corresponding scientific names (Armstrong, personal communication).

Site position and elevation were recorded with a Garmin GPSmap 60CSx unit. The heights of four to six representative trees from each canopy level were recorded using a clinometer. Mean canopy height was estimated based on these representative trees using the following categories: A, 1 m; B, 2-3 m; C, 4-5 m, D, 6 m; E, 7-8 m; F, 9-10 m; G, 11 m; H, 12-13 m; I, 14-15 m; J, 16+ m. Canopy cover was measured through the use of a spherical densitomer. The canopy connectivity was measured in two additional ways: the average distance between tree crowns in the canopy

layer(s), and the average distance between tree trunks at a height of 5 m of varying diameter at breast height (dbh) (1-5 cm, 6-10 cm, 11-20 cm, and 21+ cm dbh). This approach will capture connectivity as it is perceived by both arboreal quadrupeds (e.g. *Varecia* and *Eulemur*) and vertical clingers and leapers (e.g. *Propithecus* and *Indri*). The distance from one tree crown to the nearest tree in each canopy layer was recorded based on the average for the patch: A, connected (0 m); B, connected/small gaps[5]; C, small gap (1-3 m), D, small/medium gaps; E, medium gap (4-6 m); F, large gap (7-9 m); G, very large gap (>10 m).

For density estimates, the dbh of every tree in each plot was recorded using a dbh tape. Density estimates, however, may mask the true spatial distribution of the trunks. Spatial distribution may be an important factor in lemur movement patterns. Therefore, it was necessary to control for the spatial distribution of the trunks within each plot. Tree spacing was categorized as either equally spaced or clumped among different dbh categories: dbh = 1-5 cm, dbh = 6-10 cm, dbh 11-20 cm, and dbh >21 cm. Tree composition, total number of lianas, tree hollows, emergent trees, dead standing trees, and fallen trees were also recorded in each plot. The number and height(s) of ravinala palms were counted in each plot as indicators of past disturbance. The abundance of bamboo, longoza, and guava were also assessed by estimation based on a graded scale (0 = none, 1 = 1/4 of the plot, 2 = 1/2 of the plot, 3 = 3/4 of the plot, 4 = dense). I further noted if bamboo or longoza was adjacent to the plot. In addition, slope was measured using a clinometer, and temperature and humidity were measured using a Kestrel pocket weather station at each plot. The averages from each of these categories are presented in the Appendix.

Tree height and dbh (≥ 6 cm dbh) were measured at an interval/ratio level (meters and centimeters, respectively), using analysis of variance (ANOVA) and pairwise comparisons of patches using Fisher's PLSD post-hoc tests. Other structural attributes were measured at the nominal level via Chi-square tests. The power of the Chi-square test becomes very large with large

[5] The combination gaps are a mix of the two meaurements indicated.

sample sizes, as is the case with most of the variables measured here. To gain insight into the relative degree of association between patches and each variable, contingency coefficient C was also calculated.

Trees of Economic and Ecological Value: The total number of trees of economic and ecological value was quantified in each patch. A brief note was also made of lemurs using those particular trees in the patch. Detailed empirical findings contribute to our understanding of which single-tree species are potential primary keystone components to the sustainability of the primate communities inside of forest fragments. The rapid expansion of the human population surrounding BNR combined with elevated poverty levels has increased the demand for land and consequently has intensified the pressure on the forest. In the past, the forest suffered from small-scale illegal wood extraction, which has recently intensified to increased commercial harvesting levels of trees of economic importance. Knowing and documenting where these trees are located in the context of the habitat patches utilized by different lemurs (and animals in general) is important for making assessments on priority areas of protection in the reserve. This is especially important if those trees are also ecologically critical to primate use and movement patterns. Documenting the locations of these valued trees is then critical in being able to prevent an ecosystem collapse as a result of amplified human activity that modifies landscape properties.

Lemur community structure: Vegetation patches were also point count stations. Lemurs utilizing these different patches and structural attributes were quantified using all-day fixed radius (50 m) point counts. Although the point count survey method has primarily been used to estimate the abundance of songbird populations (Ralph et al., 1995), it is highly applicable in BNR to estimate lemur abundance and diversity. Line transect surveys are not applicable to all surveys of primate species or geographic areas due to either steep inaccessible mountainous geographic regions, dense habitat conditions, species that are rare and occur at low population densities, cryptic species, and/or time constraints (Brockelman and Ali, 1987). Prior distance sampling research confirms the

ineffectiveness of this methodology in BNR (Mertz, 2006). Point counts are conducted at a fixed location for a fixed period of time (Sutherland, 2002). This is advantageous for several reasons. The observer can concentrate solely on detecting, locating, and identifying the species of interest, patchy habitats can be sampled more easily since a predetermined transect is not followed, and a quantitative analysis of the vegetation is less difficult for a point than a line (White and Edwards, 2000). The purpose of the point count methodology is to assess the lemurs that utilize a quantified patch via the vegetation analysis proposed for this research. This is essential to determine how important each of these patches is to the lemur communities in terms of utilization and movement paths. Each point count corresponds with the vegetation plots that quantify a 50 meter radius of local habitat characteristics. The point count methodology allows for the assessment of lemur taxa that utilize the quantified patch via this vegetation analysis. The vegetation plots were visited on a monthly rotational basis for the span of this research field season. Three aspects of community structure were considered: the abundance, richness, and diversity of species. When the first lemur was detected the following were recorded: species, group composition, group number, activity, and positional behavior (see below, Behavioral Data). Simpson's Index (D) (Simpson, 1949) was used to quantify the lemur diversity in each patch. Simpson's Index is a measure that accounts for both richness and evenness. Chi-square tests were used to test for differences in patch use and behavior among the lemur taxa.

Ground reference data and geographical information systems: A powerful application of landscape ecology to gain a greater understanding of forest fragment biology lies within its maps, images, spatial statistics, and ecological modeling. Geographic information systems (GIS) is an effective tool for integrating information and depicting both real and synthetic landscape patterns (Wiens, 2002). GPS data points were collected at each vegetation patch with a hand held Garmin GPSmap 60CSx unit. This GPS model was highly effective and consistent in providing data points. In instances of dense vegetation, deep valleys, or days of low cloud cover, that inhibit the GPS from

satellite contact an external antenna was used to further allow coordinate readings. ESRI's ArcGIS 10.1 software was used to map the spatial distribution of vegetation structural patches and lemur taxa occurrence and movement. This GIS landscape model can advise land developers, based on lemur habitat preferences and movement patterns, where to restore habitat, where to protect habitat, and where to build/maintain connectivity. The concurrent use of GIS with habitat modeling accounts for spatial structure and landscape patterns, important aspects of habitat quality (Donovan et al., 1987; Rickers et al., 1995; Robinson et al., 1995). Moreover, habitat models that are GIS-based can be used to evaluate various land management scenarios and create potential distribution maps (e.g. Guisan and Zimmerman, 2000; Marzluff et al, 2002; Larson et al., 2003).

Patch boundary analysis via camera traps: Animal movement patterns as well as how and what scales (patch and/or landscape) animals change their movements in relation to their environment is central to foraging ecology, habitat selection, dispersal, and spatial population ecology (Fauchald and Tverra, 2003). It is important to understand the information that is available to an animal as it moves through its environment and how this information is used to select a patch (Lima and Zollner, 1996). For example, larger animals that move over large distances may perceive the landscape at a coarser scale and landscape context may be of primary importance. In contrast, finer scale aspects of a given patch such as branch diameter or liana density may be more influential to smaller animals. Further, the pattern of the vegetation influences an animal's perceived connectivity of the landscape (Vos et al., 2001). A species that does not cross patch boundaries into adjacent habitats will decrease its dispersal abilities and potential population size and therefore increase its extinction risk. In addition to vegetation analysis and direct behavioral observations, camera traps are an efficient means to quantify habitat use by multiple species simultaneously in different areas of the reserve. Eight Scoutguard SG550C camera traps were used. The camera traps were placed in critical areas between differing vegetation structural types (e.g. secondary and primary forest, invasive plant species) and within the eight vegetation patches defined in this

research. The cameras were moved around on a rotational basis to these different areas and fastened onto trees via a nylon belt at varying heights. Any movement of animal (or human) triggers the SG550C camera in a certain region of interest monitored by a highly sensitive Passive Infra-Red (PIR) motion sensor. Each camera was programed to take a series of three photographs anytime it was triggered so that animals moving in front of the lens would be captured. These cameras were used as tools to contribute to the behavioral component of this research by identifying which lemur taxa are or are not utilizing and/or moving through particular areas of the reserve. With improved technology and decreased costs, the use of camera traps has become increasingly useful in our understanding of where different animal species occur in an ecosystem (Tobler et al., 2008), for monitoring activity patterns (van Schaik and Griffiths, 1996), and for estimating animal density (Trolle and Kery, 2005). The images from the camera traps were managed and analyzed through Camera Base version 1.3 (Tobler, 2007).

Behavioral Data: Positional behavior consists of two types of activity, locomotor and postural behaviors (Prost, 1965). Data were collected from focal animals during the time period of each point count and during all day follows. Positional data were collected with instantaneous time samples of focal animals taken at 2-minute intervals. On each two-minute mark, the following was recorded: locomotor or postural activity, correlated behavior, the size, height, and orientation of the substrate used, and quadrant location (Sussman, personal communication) in the tree (Table 2.1; Figure 2.1). When possible, these same data were also collected for the nearest neighbor to the focal animal as well as the distance between the two individuals. Positional behavior was scored as travel-between when the movement occurs between trees and travel-within when the lemur remains in the

same tree. The distance between tree trunks and/or from one tree crown to the next that the lemurs used was recorded: A, 1 m; B, 2-3 m; C, 4-5 m, D, 6 m; E, 7-8 m; F, 9-10 m; G, 11 m; H, 12-13 m; I, 14-15 m; J, 16+ m.

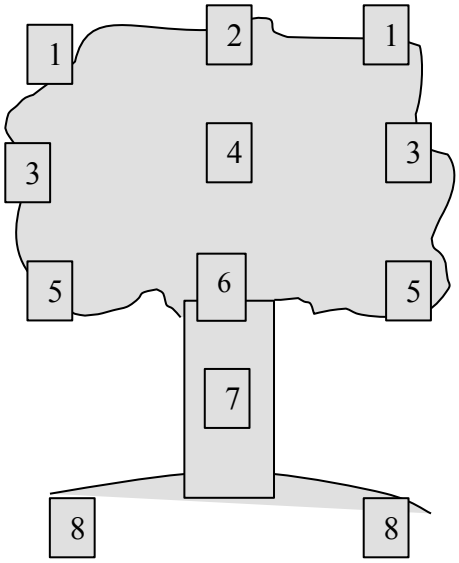


Figure 2.1 Two-dimensional representation of tree quadrants. Quadrants 2, 4, and 6 refer to the core of the tree while 1, 3, and 5 refer to the perimeter space of the tree (Sussman, personal communication).

The vegetative substrates used by the lemurs were marked with note bearing flagging tape. The date, lemur species group size and composition, and what they were doing in the tree were data recorded on the tape. This way, repeated use of trees and activity in those trees could be recorded. This provided data on the importance of local vegetation characteristics (microhabitat) within a patch to an individual lemur taxon and how this may affect the overall lemur community structure. Specific trees or structural types that were used repeatedly were considered keystone elements.

Table 2.1 Ethogram of lemur behavior in BNR

Type of Locomotion

Leaping: A movement in which the hindlimbs are used to propel an animal across a gap. This includes quadrupedal standing then leaping and vertical clinging and then leaping.
Climbing: A movement up or down a strongly oblique or vertical support or through irregular and intertwined small supports.
Quadrupedalism: A movement in which all four limbs move in a regular pattern above a support. This includes walking and running.
Quadrupedal suspensory movements: a movement where the body progresses below a support using 4 limbs.
Bridging: A movement where spatial gaps are crossed. First, the hands are stretched out to grab the new support and second, the rest of the body is stretched across and then pulled over to the new support.
Vertical Bounding: Short successive jump-clings upward along a vertical support

Postures

Sitting: To rest with the haunches lowered onto a supporting surface.
Sit Extend: To rest with the haunches lowered onto a supporting surface with the legs fully extend in front of the body with feet often grasping a vertical of oblique substrate.
Sit Tail Wrap: To rest with the haunches lowered onto a supporting surface with the tail wrapped around the front of the body and often over the adjacent shoulder.
Stand: To maintain an upright position on top of a support with legs extended (on all four limbs or bipedally).
Vertical cling: The animal grasps a vertical or strongly oblique substrate without supporting any of its weight on other branches.
Suspension: The animal hangs beneath a support suspended by two or more limbs. In lemurs, the most common suspensory posture is quadrupedal, bipedal, and tripedal (two feet and one hand) postures are also used.
Recline: To lie down on ventrum, side, or back.

Correlated behavior

Travel: Movement between a series of trees. Often will involve longer distances
Feed/Forage: Movements within a single tree
Rest: Inactivity
Groom Self: Clean, maintain one's body via licking, scratching, or use of a toothcomb
Groom Other: Clean, maintain another's body via licking, scratching, or use of a toothcomb

Substrate

Support size: A, Very Small < 1cm; B, Small = 1-5cm; C, Medium 6-10cm; D, Large 11-15cm, E, Very Large 16+
Orientation: A, Horizontal (0-15 degrees); B, Oblique (15 to 75); C, Vertical (75-90).

Location

Height of substrate: A, 1m; B, 2-3m; C, 4-5m, D, 6m; E, 7-8m; F, 9-10m; G, 11m; H, 12-13m; I, 14-15m; J, 16+m

Connectedness

Canopy Distance: A, connected (0m); B, connected/small gaps; C, small gap (1-3m), D, small/medium gaps; E, medium gap (4-6m); F, large gap (7-9m); G, very large gap (>10m).

***Radio collars*:** Telonics radio collars were used to add another dimension to create a realistic landscape model to understand lemur movement patterns and occupied areas across the landscape. The use of the collars was critical to understanding habitat use and movement patterns given the steep undulating terrain of BNR and extreme difficulty in successfully following arboreal lemurs in BNR. One individual from each group was fitted with a size appropriate radio collar. Two groups of *Propithecus diadema diadmena*, five groups of *Indri indri*, and one group of *Eulemur fulvus albifrons* were followed on a rotational basis over the course of this research. Each group was followed for two consective days on a monthly basis. While following these groups, GPS points were taken with a hand held Garmin GPSmap 60CSx unit. The activity of the lemur was recorded for each GPS point recorded (e.g. eating leaves, moving, resting, etc.). A tracking feature on this unit also allowed for a continuous stream of latitude and longitude data points to be recorded essentially tracing the path of movement for each group on a daily basis. The GPS points of these paths were then uploaded into a GIS database. These data were overlaid onto the Betampona map to have a better understanding of movement patterns of the different lemur groups. These data collected by following the radio collared lemurs contributed to the GIS landscape model that will advise land developers, based on lemur habitat preferences and movement patterns, where to restore habitat, where to protect habitat, and where to build/maintain connectivity.

All darting was conducted by Dr. Randy Junge (M.S., D.V.M., DiplA.C.Z.M), the Director of Animal Health and Nutrition and lead veterinarian of the Saint Louis Zoo. Each lemur was anesthetized using tiletamine and zolazepam (Telazol®, Fort Dodge Animal Health, Overland Park, Kansas 66225, USA; 10-20 mg/kg, i.m.) by dart (Type "C" Disposable Dart, Pneu-Dart, Williamsport, Pennsylvania 17701, USA). After the anesthesia took effect, the lemurs were caught in large hockey nets with the help of a Malagasy team. Once anesthesia was stable, a complete physical examination was performed, and rectal temperature, heart rate, respiratory rate, and body weight were measured. This information, in addition to collection of any ecto-parasites and blood, was obtained

as part of the larger Prosimian Biomedical Survey Project that is designed to assess the health of populations of free-ranging lemurs in Madagascar (Junge, personal communication). One animal from each group was fitted with a radio collar. Once the lemur had recovered from anesthesia, it was returned to the original capture site and released on the same tree it was darted on.

Data were collected from focal animals during all day follows. All day follows were conducted on a rotational basis with point counts. The lemur group followed was also conducted on a rotational basis with the other groups. Data were collected from focal animals during the time period of each point count and during all day follows. Positional data were collected with instantaneous time samples of focal animals taken at 2-minute intervals, following the same protocol as that described in the paragraph above on behavioral data. During all day follows of the radio-collared lemurs a quick habitat assessment was also made for each area the lemurs used and/or moved. Data were collected on the heights of the different canopy levels and the size of the gap (Connected = 0 m, Small gap = 1-3 m, Medium gap = 4-6 m, Large gap = 7-9 m, Extra Large gap >10 m), if trees were clumped or equal at three different dbh divisions (6-10 cm, 11-20 cm, and 21+ cm) and the distance between the trees at each division. Similar to the point-counts, the vegetative substrates used by the lemurs were marked with flagging tape indicating the date, lemur group, and what they were doing in the tree. In addition, vegetation plots (see section above on vegetation plot methodology) were later established in the primary areas the different lemurs were utilizing to provide a more detailed habitat assessment.

***Radio-collared Lemur Groups*:** These taxa and groups were chosen because of the interesting and highly relevant comparison. *Propithecus* is somewhat of a specialist in terms of requiring high quality food and locomotes by vertical clinging and leaping. At Mantadia, similar to other *Propithecus* spp. (Richard, 1978; Wright, 1987; Hemingway, 1998), *P. d. diadema* showed a preference for fruits and seeds (39.2%) as well as flowers (15.5%), but also consumed immature leaves 42.1% of the time (Powzyk and Mowry, 2003). *Propithecus d. diadema* relied on readily

digestible foods high in fat and water-soluble carbohydrate content (Powzyk, 1997:115). This could be a result of their high-energy lifestyle, including patrolling extensive territories and scent marking (Powzyk and Mowry, 2003). Although results from a year-long study in Tsinjoarivo, eastern Madagascar on four groups of diademed sifakas (*P. d. diadema*) indicates that these lemurs have the ability to "cope" and are behaviorally flexible in terms of group cohesion. Diademed sifakas live in female dominated, multi-male multi-female groups of up to eight individuals (Powzyk, 1997). But groups living in forest patches were observed to have less group cohesion than groups living in continuous forest (Irwin, 2007). The reduced group cohesion of the fragment groups is a result of the patchy distribution of food resources in the smaller forests (Irwin, 2007). *Propithecus* is the rarest (~21 individuals) and most elusive lemur in BNR. The two focal sifaka groups chosen for this research inhabit different areas of the reserve. Sifaka group 1 occupies the central and northern portion of the reserve traversing through stretches of primary forest. This group consisted of one adult male and two adult females. The second sifaka group, group 10, inhabits the southern portion of the reserve with the limits of their territory abutting the degraded southern portion of BNR. This group consists of one adult male, one adult female, and one juvenile female.

Indri belong to the same taxonomic family as *Propithecus* (Indriidae) and also locomote by vertical clinging and leaping, but in comparison to sifaka, are more folivorous and are also more abundant in BNR (~100 individuals). The geographic range of *I. indri* and *P. d. diadema* in Madagascar was very similar (Tattersall, 1982), although in more recent years local extinctions in forest fragments and increased hunting pressures as a function of the political instability, may result in changes in the extent of each taxa's range (IUCN, 2012). The latter are capable of a sympatric co-existence due to partitioned feeding behavior (Powzyk, 1997). Both indriids are essentially folivores but, as mentioned prior, *P. d. diadema* has a "heightened preference for seeds, whole fruits, and flowers" (Powzyk and Mowry, 2003:1155), whereas *Indri* consume mainly

immature foliage (72.3% of feeding time). At Mantadia National Park (10,000 hectares of relatively undisturbed habitat), *I. indri* and *P. d. diadema* are abundant (Powzyk, 1997; Powzyk and Mowry, 2003). *Propithecus* actually maintain a higher density of individuals per square kilometer (10.5) than *Indri* (5.2). In comparison, *I. indri* at Betampona is also highly folivorous with leaves and petioles accounting for 82% of its diet, feeding on at least 42 plant species (Britt et al., 2002).

Female *Indri indri*, along with *Propithecus diadema diadema*, are the largest living lemurs (6.48 kg) (Powzyk, 1997). Despite this large body size, *Indri* is relatively abundant at Betampona. The dietary range of *Indri* (leaf specialists) with less dependence on patchily distributed food (Powzyk and Mowry, 2003), as well as local taboos[6] against hunting, collectively may contribute to the indris' more elastic response to environmental change (Britt et al., 2003a).

Indri usually live in small family groups that consist of two adults with young (Powzyk and Thalmann, 2003). However, in smaller forests larger group sizes have been reported due to the inability to disperse (Pollock, 1975). The focal *Indri* groups for this research in BNR are interesting in that group composition and size are different among the five study groups. The groups, discussed in more detail below, vary from one solitary adult female to a group of five consisting of one adult male, three adult females, and one juvenile male.

In contrast to the indriids, *Eulemur fulvus* is an arboreal quadruped and the most abundant lemur taxon (~300 individuals) in BNR. *Eulemur fulvus* reside in small groups that consist of multiple males and females (Overdorff and Johnson, 2003). These groups express tight group cohesion and tend to be territorial (Overdorff and Johnson, 2003). *Eulemur fulvus* is ecologically and behaviorally flexible (Overdorff and Johnson, 2003) and are found in almost every forested area of Madagascar (Tattersall and Sussman, 1998). *Eulemur fulvus* is frugivorous and is capable of exploiting over 100 plant species, but can also focus on 5 to 15 plant species each month (Overdorff and Johnson, 2003). Brown lemurs select a variety of foods over the course of a year according to

[6] The local taboos against eating Indri have started to break down in Madagascar.

their seasonal or monthly availability, thus accessing foods with consistent quality (Tarnuad, 2006). Furthermore, members of the genus *Eulemur* exhibit cathemeral activity (Tattersall, 1987) and eastern brown lemurs have been observed engaging in activity across 24-hour periods throughout the year (Rasmussen, 1999). The brown lemur group focused on for this research consisted of one adult female and two male juveniles. The group primarily fed, traveled, and slept in the southern portion of the reserve using some of the degraded habitat.

Differences in habitat use and resting, feeding, and moving behaviors were measured with Chi-square and Kolmogorov-Simirnov statistical tests. The lemur groups are named after their respective receiver channels that correspond with the radio collar's transmitting frequency.

Focal Lemur Groups:

PROPITHECUS GROUP 10: Group composition consists of one adult male, one adult female, and one juvenile female that was approximately one year old at the time of the research.
Adult male fitted with radio collar. Female fitted with pink dog collar.
Female 6.7 kg, body length 47.5 cm, tail length 50 cm
Male 5.6 kg, body length 43 cm, tail length 45 cm

PROPITHECUS GROUP 1: Group composition consists of one adult male and 2 adult females. Both adult females in the group gave birth although only one of the infants survived past 3 months.
Male purple dog collar. 6.0 kg, body length 49 cm, tail 49 cm.
Female radio collar. 6.0 kg, body length 49 cm, tail 50 cm
Female no collar. No capture.

EULEMUR GROUP 34: Group composition consists of one adult female and 2 juvenile males. One juvenile appeared to be younger than the other based on body size and also dependency to the adult female in the form of close spatial proximity.

Female radio collar. 2.5 kg, body length 34.6 cm, tail length 53.9 cm

Males no collar. No capture.

INDRI GROUP 40: Group composition consists of one adult solitary female.

Female radio collar. 7.5 kg, body length 52 cm, tail length 5 cm

INDRI GROUP 50: (new group) Group composition consists of 1 adult male, 3 adult females and one juvenile male.

Male radio collar. 6.5 kg, body length 44.0 cm, tail 6 cm.

Female green collar. 6.6 kg, body length 50 cm, tail length 6.5 cm.

Juvenile male no collar. 3.3 kg, body length 41.5 cm, tail 4.5 cm.

Female no collar. 7.1 kg, body length 53.0 cm, tail 7.0 cm.

Female light blue/teal collar. 5.4 kg, body length 52 cm, tail 5.8 cm.

INDRI GROUP 55: Group composition consists of 1adult female, 2 adult males, 1 male juvenile.

Male radio collar. 6.5 kg, body length 49 cm, tail 3.7 cm.

Female blue dog collar. 7.3 kg, body length 5.3 cm, tail length 5.3 cm.

Male pink collar. 5.9 kg, body length 43.5 cm, tail length 6.0 cm.

Juvenile no collar. No capture.

INDRI GROUP 45: Group composition consists of one adult female and one adult male

Female radio collar. 6.8 kg, body length 51.0 cm, tail length 4.3 cm

Male purple dog collar. 6.0 kg, body length 47 cm, tail length 5.0 cm.

INDRI GROUP 14: Group composition consists of one adult female, one adult male, and one female juvenile.

Female radio collar. 8.4 kg, body length 57.0 cm, tail length 4.0 cm.

Male faded red collar with gold medallion. 7.3 kg, body length 51.0 cm, tail length 3.9 cm.

Female juvenile no collar. 3.8 kg, body length 46.5 cm, tail length 3.0 cm

CHAPTER 3
ANALYSIS OF EIGHT QUANTIFIED PATCHES

Overview of Chapter

This chapter focuses on the question: Are there quantifiable differences between the patches? If so, what are the differences? A detailed assessment of the structural variation within BNR was necessary for the development of a framework within which to work, while also effectively representing the spatial component of this research. In an effort to understand more about the effects of anthropogenic change on biodiversity, there is a focus on quantifying structure and habitat use (e.g. Dagosto and Yamashita, 1998; Warner, 2002; Schwitzer et al., 2007; Boyle and Smith, 2010; Chagas and Ferrari, 2010; Pyritz et al., 2010; Herrera et al., 2011; Hardus et al., in press). However, these studies usually evaluate a stark dichotomy between primary and secondary, logged or unlogged, continuous or fragmented and ignore the heterogeneity that exists within each of these categories or across the landscape. The goal of this chapter is to establish a spatial framework with detailed vegetation structural analysis of a forest fragment to facilitate research concerning movement and differential patch use among lemurs. This is necessary in order to assess the spatio-temporal variability in the distributions and survival of lemurs in a heterogeneous forest fragment. Species persistence patterns and population viability in modified, heterogeneous forests depend on a detailed assessment of forest structure and the quantification of spatial heterogeneity (Haila et al., 1989, 1996; Niemela et al., 1996; Turner, 2005). This type of analysis allows meaningful statements regarding variation in patch structure and why organisms occur where they do or move as they do in a landscape. Four 10 m x 10 m plots were placed within a 50 meter radius at each of eight designated locations throughout BNR (see methodology chapter for more detailed description). These four quantified plots collectively represent a single patch, or habitat type, in the landscape. Thus, the patch description and counts of trees are abundances within this 50 meter radius.

The first section of this chapter provides a statistical comparison of the different attributes quantified within the patches. Analysis of variance (ANOVA) and Chi-square tests indicate that there are significant differences between the patches in every attribute measured. The remaining eight sections discuss the quantitative descriptions of each of the patches, highlighting the main components that define the patch as a collective, distinct spatial unit concurrently separating it from other patches within the landscape. A comparison is also made for each patch in relation to the other patches at the end of the descriptive section, emphasizing the major quantified differences, which ultimately may impact biodiversity.

The quantitative description of each of the patches includes data about each of the following:

a. Structure (canopy height, number of canopy layers, densities of categorized dbh trees of varying girth, spatial arrangement of the trees, connectedness of canopy, number of emergent trees, new growth in the form of herbaceous shrubs and treelets).

b. Temperature and humidity.

c. Trees of economic and ecological importance.

d. Tree composition of most abundant taxa found in patch.

e. Discussion of the context of the patch with respect to the surrounding environment.

f. GIS map to illustrate location of the different patches in BNR.

g. Comparison of important vegetative attributes within a patch in comparison to other patches.

Trees of value were measured to contribute to a database that can assess the risk factor for the biodiversity of the patch. The rapid expansion of the human population surrounding BNR combined with elevated poverty levels has increased the demand for land and consequently has

intensified the pressure on the forest. In the past the forest suffered from small-scale illegal wood extraction, which has recently intensified to increased commercial harvesting levels of trees with significant economic value. Knowing and documenting where these trees are located in the context of the habitat patches utilized by different lemurs (and animals in general) is important for making assessments on priority areas of protection in the reserve, especially if those trees are also ecologically critical to primate use and movement patterns. Documenting the locations of these valued trees is then also important in preventing an ecosystem collapse as a result of amplified human activity that modifies landscape properties. The following is a list and description of these trees of economic importance that were documented in each patch. These trees will be referred back to throughout this chapter as each patch is discussed in detail. The descriptive information of each of the plant taxa is adopted from Armstrong (personal communication, 2007) that includes her reference to the Generic Tree Flora of Madagascar by George Schatz (2001) and the associated Malagasy names based on analysis and conversations with Madagascar Fauna Group conservation agents.

Hazomafana (*Diospyros* sp.): The larger hazomafana trees are often harvested for their valuable ebony wood and for various tourist souvenirs such as jewelry boxes or carved statues of lemurs, chameleons, or other Malagasy animals. The fruits of hazomafana trees are also an important food source for frugivorous animals.

Hazomainty (*Diospyros* sp.): Hazomainty trees are small to large hardwood trees. The largest trees yield ebony hardwood used for construction and for tourist souvenirs.

Hasina (*Dracaena* sp.): Hasina can be shrubs to medium-sized sparsely branched trees. The flowers of this tree are edible and sometimes sold.

Mampay (*Cynometra* sp.): Mampay trees can be small to large reaching heights of 30 meters with buttresses. The wood is used in construction and the white flowers and seeded fruits are important food items for lemur taxa when they are seasonally available.

Ramy (*Canarium* sp.): Ramy wood is also harvested for construction (e.g. pirogues). In addition, the resin is used to treat urinary tract infections and to caulk boats. Ramy fruit is edible and the seeds are rich in oil thus attracting a variety of animals including humans.

Ravinala (*Ravenala madagascariensis*): Ravinala palm fronds are used as building materials. The fronds are dried and then used for roofing material and just the stem (stripped of the leaf) is used to build the walls of the house. Ravinala initially establish themselves in light gaps. Lemurs consume the nectar, flowers, and seeds, of the ravinala.

Pallisandre (*Dalbergia* sp.): Pallisandre (or rosewood) trees are harvested for their reddish hardwood that is used for ornamental furniture, tourist souvenirs, and construction.

Azinina (*Symphonia* sp.): Azinina trees have orange/red fleshy waxy flowers and edible ovoid fleshy fruits. These are sold at market.

Guava (*Psidium cattleianum*): Guava is a highly invasive plant that forms dense thickets that shade-out and suffocate native vegetation. Guava is cultivated throughout Madagascar for its fruits.

Longoza (*Aframomum angustifolium*): Longoza is a cardamom plant resulting from past agricultural encroachment inside of the reserve. This plant colonizes open gaps in the forest and can be found growing in varying sized patches to just a few single plants growing randomly throughout the forest. Longoza can grow up to 2.0 to 2.5 meters tall and there can be as many as 10 stalks in one square meter. I am unaware of the economic importance of this plant to local communities residing near BNR. However, this plant is used to make spices or medicinal treatments in other African countries. In the United States, a cosmetic conglomerate claims that the seed extract contains anti-aging properties, which may result in an increase harvest of this plant.

Zanamena (*Dialium unifoliolatum*): Zanamena are large trees with very hard wood and edible large fleshy fruits.

Fanzana (*Cyathea* sp.): A majority of the larger species are considered endangered due to over-exploitation for their trunks. The basal portions are hollowed out and sold as planters.

Voasirindrina (*Sorendea* sp.): Fruits are edible and sold at the market.

Afomena (*Dombeya* sp.): Afomena are shrubs to small trees often found in degraded forest or in light gaps in primary forest. Afomena trees are shade intolerant. I am unaware of the economic value of this plant.

Molanga (*Dombeya* sp.): Molanga trees are often found in degraded areas or in light gaps in primary forest. I am unaware of the economic value of this plant.

STATISTICAL COMPARISON OF PATCHES BY ATTRIBUTE

ANOVA

Tree height and dbh (≥ 6 cm dbh) were measured in meters and centimeters, respectively. Analysis of variance (ANOVA) indicates that these attributes differ significantly among the patches (height, Tables 3.1, 3.2, $F_{7,240}=5.689$, $p<0.0001$; dbh, Tables 3.3, 3.4, $F_{7,718}=2.278$, $p<0.027$). Box plots for height and dbh are depicted in figures 3.1 and 3.2, respectively. Pairwise comparisons of patches using Fisher's PLSD post-hoc tests are listed in Tables 3.5 and 3.6 for height and dbh, respectively.

Table 3.1 ANOVA Table for height (m)

ANOVA Table for Height (m)

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Patch	7	695.414	99.345	5.689	<.0001	39.825	1.000
Residual	240	4190.865	17.462				

Table 3.2 Descriptive statistics for height (m)

Means Table for Height (m)
Effect: Patch

	Count	Mean	Std. Dev.	Std. Err.
1600	32	9.433	2.406	.425
800-900	25	7.928	3.191	.638
Betakonona	40	9.466	5.070	.802
Fara	55	11.369	5.579	.752
Guava	19	5.849	2.487	.571
Sahabefoza	39	7.046	3.403	.545
Sahakoho	23	9.174	4.385	.914
Zubenubi	15	9.625	2.796	.722

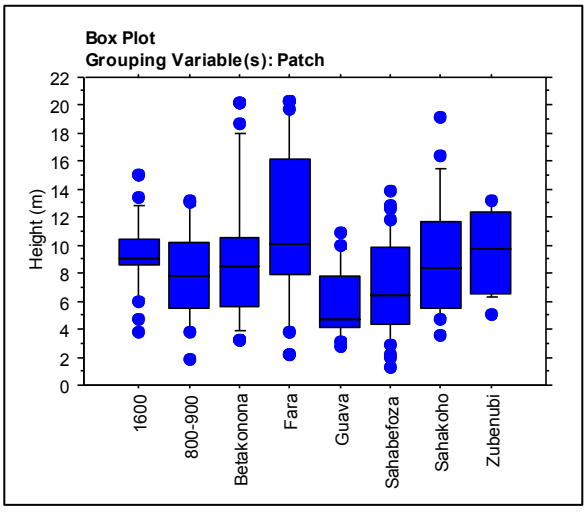


Figure 3.1 Box plot for height (m)

Table 3.3 ANOVA Table for dbh (cm)

ANOVA Table for dbh (cm)

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Patch	7	1286.429	183.776	2.275	.0270	15.922	.847
Residual	718	58011.113	80.795				

Table 3.4 Descriptive statistics for dbh (cm)

Means Table for dbh (cm)
Effect: Patch

	Count	Mean	Std. Dev.	Std. Err.
800-900	103	12.621	9.474	.933
Betakonona	104	14.913	11.135	1.092
Fara	77	15.913	10.628	1.211
Guava	38	12.737	7.934	1.287
PP1600	79	13.481	7.442	.837
Sahabefoza	100	12.160	7.465	.747
Sahakoho	131	13.237	7.458	.652
Zubenubi	94	11.521	9.335	.963

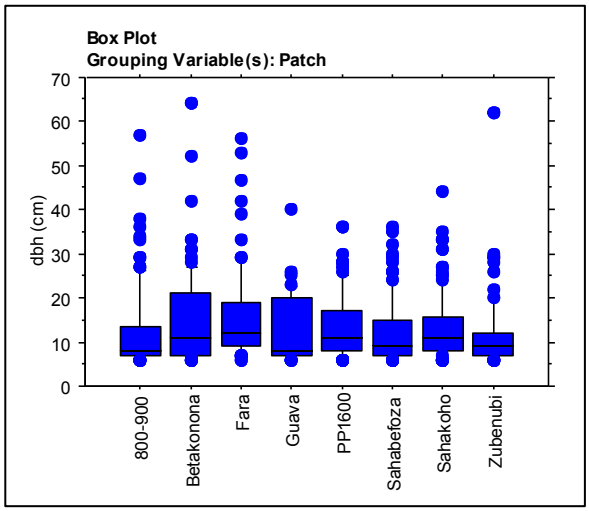


Figure 3.2 Box plot for dbh (cm)

Table 3.5 Fisher's PLSD for height (m)

Fisher's PLSD for Height (m)
Effect: Patch
Significance Level: 5 %

	Mean Diff.	Crit. Diff.	P-Value	
1600, 800-900	1.505	2.197	.1785	
1600, Betakonona	-.034	1.952	.9728	
1600, Fara	-1.936	1.830	.0382	S
1600, Guava	3.584	2.384	.0034	S
1600, Sahabefoza	2.386	1.963	.0174	S
1600, Sahakoho	.259	2.250	.8210	
1600, Zubenubi	-.192	2.576	.8832	
800-900, Betakonona	-1.539	2.099	.1499	
800-900, Fara	-3.441	1.986	.0008	S
800-900, Guava	2.079	2.505	.1035	
800-900, Sahabefoza	.881	2.109	.4114	
800-900, Sahakoho	-1.246	2.378	.3029	
800-900, Zubenubi	-1.697	2.688	.2148	
Betakonona, Fara	-1.902	1.711	.0294	S
Betakonona, Guava	3.618	2.294	.0021	S
Betakonona, Sahabefoza	2.420	1.852	.0107	S
Betakonona, Sahakoho	.292	2.154	.7893	
Betakonona, Zubenubi	-.159	2.492	.9003	
Fara, Guava	5.520	2.191	<.0001	S
Fara, Sahabefoza	4.322	1.723	<.0001	S
Fara, Sahakoho	2.195	2.044	.0354	S
Fara, Zubenubi	1.744	2.398	.1533	
Guava, Sahabefoza	-1.198	2.303	.3066	
Guava, Sahakoho	-3.325	2.552	.0109	S
Guava, Zubenubi	-3.776	2.843	.0094	S
Sahabefoza, Sahakoho	-2.127	2.164	.0540	
Sahabefoza, Zubenubi	-2.579	2.501	.0434	S
Sahakoho, Zubenubi	-.451	2.732	.7453	

Table 3.6 Fisher's PLSD for dbh (cm)

Fisher's PLSD for dbh (cm)
Effect: Patch
Significance Level: 5 %

	Mean Diff.	Crit. Diff.	P-Value	
800-900, Betakonona	-2.292	2.453	.0670	
800-900, Fara	-3.292	2.659	.0153	S
800-900, Guava	-.115	3.349	.9461	
800-900, PP1600	-.860	2.639	.5227	
800-900, Sahabefoza	.461	2.477	.7148	
800-900, Sahakoho	-.615	2.324	.6034	
800-900, Zubenubi	1.100	2.517	.3912	
Betakonona, Fara	-1.000	2.653	.4598	
Betakonona, Guava	2.177	3.345	.2018	
Betakonona, PP1600	1.432	2.634	.2860	
Betakonona, Sahabefoza	2.753	2.472	.0291	S
Betakonona, Sahakoho	1.677	2.318	.1559	
Betakonona, Zubenubi	3.392	2.511	.0082	S
Fara, Guava	3.176	3.499	.0751	
Fara, PP1600	2.432	2.826	.0916	
Fara, Sahabefoza	3.753	2.676	.0060	S
Fara, Sahakoho	2.676	2.534	.0385	S
Fara, Zubenubi	4.392	2.712	.0015	S
Guava, PP1600	-.744	3.484	.6751	
Guava, Sahabefoza	.577	3.363	.7364	
Guava, Sahakoho	-.500	3.252	.7629	
Guava, Zubenubi	1.216	3.392	.4820	
PP1600, Sahabefoza	1.321	2.656	.3292	
PP1600, Sahakoho	.244	2.514	.8487	
PP1600, Zubenubi	1.960	2.694	.1536	
Sahabefoza, Sahakoho	-1.077	2.343	.3674	
Sahabefoza, Zubenubi	.639	2.535	.6210	
Sahakoho, Zubenubi	1.715	2.385	.1584	

CHI-SQUARE

Chi-square tests reveal that each attribute varies significantly among the patches ($p<0.0001$ in all cases). The power of the Chi-square test becomes very large with large sample sizes, as is the case with most of the variables measured here. To gain insight into the relative degree of association between patches and each variable, contingency coefficient C was also calculated. Contingency coefficient C is a nominal measure of correlation that is sensitive to sample size and is used here to rank the attributes by strength of association. Because the maximum value C can take is dependent on the size of the chi-square matrix and is often less than 1.0, all C-values were converted into a percentage-of-maximum value. These values are listed in Table 3.7. Total counts of each attribute are provided in Table 3.8.

Table 3.7 Chi-square, C, and % of Max values for patch attributes

Attribute	X^2 Value	p	C	% of Max*
Ravinalas	100.8	<0.0001	0.76	80.7
Lianas	1117.6	<0.0001	0.75	80.1
Dead fallen and Standing Trees	65.3	<0.0001	0.69	74.3
Palms	50.4	<0.0001	0.58	62.3
1 to 5cm dbh	445.2	<0.0001	0.52	55.6
New growth vegetation 0 to 2 meters	284.4	<0.0001	0.40	43.1

*C_{Max} = 0.94 in all cases

Table 3.8 Total counts of patch attributes

Total Count of Attributes in Patch						
Patch	Palms	Dead fallen/standing trees	Liana	New growth	1 to 5 cm dbh	Ravinala
Sahakoho	25	1	24	144	122	12
Guava	5	10	43	171	378	33
Zubenubi	3	21	439	83	51	1
Betkonona	13	6	74	151	132	0
800-900	16	24	41	130	127	19
Fara	7	1	66	329	106	0
1600	3	2	100	156	171	2
Sahabefoza	26	5	84	304	116	9

A map of the location of each of the patches is provided below (Figure 3.3).

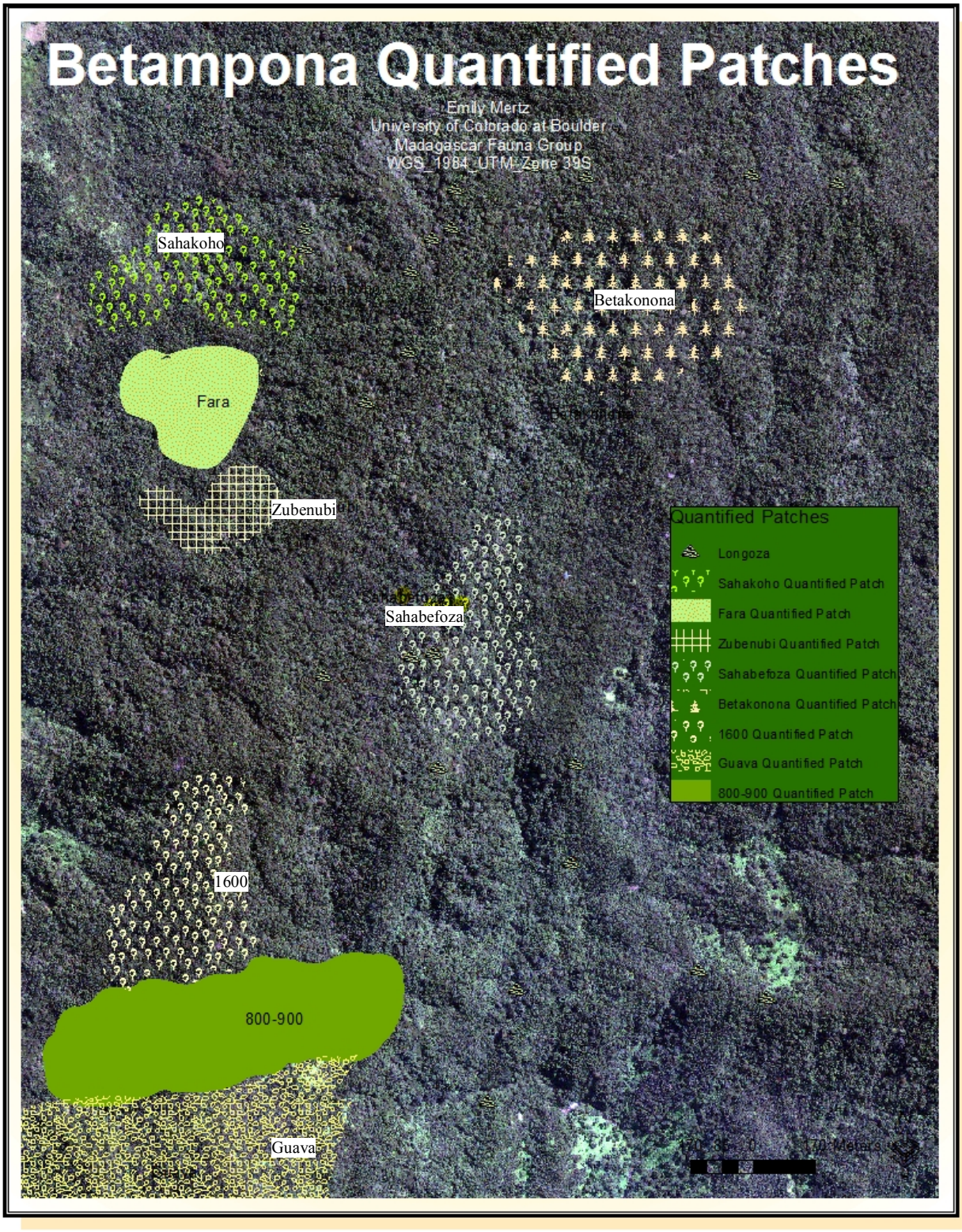


Figure 3.3 Map of quantified patch locations in BNR. The patch names correspond to meter locations along the trail, the major plant composition of the area, or local Malagasy designations for an area.

GUAVA PATCH: Guava (*Psidium cattleianum)* is a highly invasive plant that forms dense thickets that shade-out and suffocate native vegetation making it difficult for other species to coexist and overtime becomes the dominant plant species. Guava was initially planted in BNR as a source of fruit for human consumption. It has now taken over parts of the forest. The guava predominately grows along the southern perimeter of the reserve with dense thickets growing 800 meters into the forest. In its thickest parts, the guava now dominates the area in species composition. The other main tree that grows in and around the guava is the ravinala palm. Ravinala palms are distinguishable by their large banana like leaves that are arranged in a fanlike single plane. The leaves are often used as building materials for the walls and roofs of Malagasy gheets (houses). Ravinalas initially establish themselves in light gaps in the forest and are often multi-trunked, growing in clusters in secondary forest. The trunk height can vary from a couple of meters to 12.5 meters. The trunk diameter often has a dbh of over 20 cm. The guava has spread throughout the reserve and now grows in isolated pockets. This plant is predominately being dispersed by lemurs and birds that eat its fruits. If the guava thickets continue to grow and expand, they could continue to suppress native forest regeneration. This will dramatically change the plant composition in these newly colonized areas.

The vegetation plots of this patch were in the southwestern portion of the reserve approximately 500 meters into the forest where the guava is at its thickest. The guava thickets extend north to 700 meters and at around 850-900 meters become more sparsely distributed. Ravinala palms become dominate. At 1000 meters the forest canopy height begins to increase along with an increase in plant species diversity. The guava extends south to the forest edge where the forest vertical space is more sparse and degraded, yet the forest floor is full, embedded with overgrown liana tangles, trees falls, and dead palm leaves. The local village, Rendrirendry, abuts the forest edge at the southern border.

There are three canopy layers that range from being connected to having medium gaps. The

first canopy layer averages 3.7 meters, the second 4.6 meters, and the third more sporadic inconsistent layer, 8.3 meters. Emergent trees average 8.6 meters with approximately one tree every 100 m^2. Canopy cover is variable, primarily influenced by ravinala palm frond extension and can range from 95.3% to as little as 25.0%. This area is very "choppy" in terms of the canopy coverage and can be quite different just by moving one step to the left or right. At 500-550 meters inside of the reserve there is primarily a single canopy layer of 4.1 – 4.7 m connected guava thickets. Guava trunk and branch dbh ranges from 5 – 7 cm. There can be as many as 134 guava plants in a 100 m^2 plot. There is also new guava growth on the forest floor of young 0.3 to 0.6 m in height plants. The branches grow several centimeters apart and often intertwine to create impenetrable areas to a human. Lianas (10.8/100 m^2, range 9-14) also grow here adding further complexity to the tangled vegetation. There is no clear vertical space in this area from the ground up to 4.7 meters. Some of the ravinala trunks are a mere one meter in height with their long palm fronds reaching the guava canopy further masking the vertical space.

Non-guava trees are often the same height as the guava canopy with some trees reaching 6.9 meters. Non-guava, 1-5 cm dbh trees can range in number from 1 to 19 in a 100 m^2 plot with the larger dbh trees being sparse. The tallest trees are the occasional ~10 meter ravinala palms that also have the larger dbh's (21+ cm). The number of ravinalas in a plot can range from three to as many as twelve. Ravinala tend to grow in clumps in the guava growing both less than 0.30 m from one another and up to a distance of 2.8 meters and 3.8 meters. Trees were identified when possible within each 100 m^2 plot. The most common trees and shrubs within the guava patch consist of guava, ravinala, ambonambona, hazoambo, and tsipatika (Table 3.9).

Trees of Economic and Ecological Value in the Guava Patch

Thirty-three ravinala trees (*Ravenala* sp.), 339 guava trees, and two hazomafana (*Diospyros* sp.) trees were identified. All have economic value to humans. All have ecological value as well. The brown lemurs using this patch ate the fruits of the hazomafana trees. The brown lemurs also

utilized these trees to move and rest. The ravinala palms in the guava are important trees for the lemurs both for movement and as a food resource. The brown lemurs frequently used the ravinala palms to move quadrupedally as they negotiated their way through the erratic nature of the guava canopy. The lemurs also consumed the nectar, flowers, and seeds of the ravinala on a regular basis. Finally, the lemurs used the ravinala palm fronds or even the seed-pods as resting/sleeping areas. The guava was not in bloom over the course of this research and so the importance of the guava fruit to the lemurs was undocumented.

Table 3.9 Common trees found in the Guava Patch

PATCH	MALAGASY TREE	NUMBER	FAMILY	SPECIES
GUAVA	AMBONAMBONA	10	ARALIACEAE	*POLYSCIAS SP*
GUAVA	LIANNA	34	?	*?*
GUAVA	GUAVA	339	MYRTACEAE	*PSIDIUM CATTLEIANUM*
GUAVA	HAZOAMBO	5	ANNONACEAE	*XYLOPIAS SPP*
GUAVA	LENDENA	4	GENTIANACEAE	*ANTHOCLEISTA AMPLEXICAULIS*
GUAVA	MAKARANANA	8	EUPHORBIACEAE	*MACARANGA HISPIDA*
GUAVA	RAVINALA	33	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
GUAVA	SADOKA BERAVINA	6	RUBIACEAE	*GAERTNERA SP*
GUAVA	SADOKA KELIRAVINA	4	RUBIACEAE	*GAERTNERA SP*
GUAVA	TARANTANA	4	ANACARDIACEAE	*MICHRONYCHIA MACROPHILIA*
GUAVA	TSIPATIKA	14	MORACEAE	*STREBLUS SPP*
GUAVA	VINTANONA	4	CLUSIACEAE	*CALOPHLLUM SP*

Temperature and Humidity in the Guava Patch

Temperature and humidity were measured with a Kestral pocket weather station at 8:00 AM, 12:00 PM, and 3:00 PM at each of the patches. The temperature ranged from 62.2 to 83.0 degrees Fahrenheit with the hottest temperatures in June, October, and November (Table 3.10). The humidity ranged from 72.4% to 100% with the highest humidity occurring in July, August, and September. The lowest humidity occurred in June and November. The guava patch has one of the highest temperature averages overall (with patch Sahakoho) compared to the other patches. Both of these patches are relatively close forest edge, which may influence temperature.

Table 3.10 Averages of daily temperature and humidity fluctuations in Patch Guava

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	89.5%	89.8%	88.8%
TEMPERATURE AVERAGE	68.4°F	72.1°F	72.7°F

Guava Patch Comparison

The guava patch is the only patch to have such a high density of guava trees. The guava has the lowest number of 1-5 cm and 11-20 cm dbh trees and one of the lowest numbers of 6 to 10 cm and 21+ cm dbh trees (Table 3.11). A majority of the larger dbh trees were ravinala palms. The lack of 1-5 cm dbh non-guava trees may be due to the large abundance of 1-5 cm dbh guava trunks, which monopolize the space and subsequently suffocate out other non-guava vegetation. There is also a fairly high density of lianas in comparison to the other patches contributing to the dense understory vegetation (Table 3.14).

Table 3.11 Average number of varying dbh trees within 100 m^2 in the guava patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20CM DBH	21+ CM DBH
9.8 (RANGE 1 - 19)	6.3 (RANGE 2 - 9)	1.2 (RANGE 2 - 9)	1.6 (RANGE 0 - 4)

The height of the first canopy layer is among the lowest of any of the patches. The heights of the second and third layers are also much shorter in comparison to the second and third layers of the other patches (Table 3.12). The third layer is inconsistent most likely because it is emergent relative to the other trees. The first canopy layer is connected similar to the other patches but what is different is that there is an abrupt jump to large gaps in the taller canopy. The guava also has the widest gaps among the taller canopy.

Table 3.12 Average canopy heights in guava patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	EMERGENT TREES (LAYER 3)
3.7 M (RANGE 3.1 – 4.1)	4.6 M (RANGE 4.1 – 5.1)	8.3 M (RANGE 6.3 – 11.0)

In most of the patches the 6-10 cm dbh trees are ≤ 1 meter apart and equally distributed but in the guava these trees tend to be more clumped from <1 meter to 2 to 3 meters apart (Table 3.13). Again, this is most likely due to the overgrown guava thickets. There is no clear vertical space in this area from the ground up to 4.7 meters and the clumped nature of the trees may impede movement of larger bodied animals within this patch or movement through this patch to an adjacent area. In contrast, perhaps small-bodied animals that seek refuge in dense vegetation for locomoting, resting, or feeding would readily utilize this patch.

The total number of ravinala palms (N=33) was higher than in other patches. The ravinalas growing in the guava had some of the tallest heights (range 10.3 m – 13.0 m). The total number of herbaceous new growth plants (0 to 2 meters) was relatively high (N=171) (Table 3.8), although this attribute varies less intensely among the patches (% of max = 43.1). The most common trees here consist of the guava, ravinala, liana, and tsipatika (Table 3.9).

Table 3.13 Spatial distributions of trees of varying dbh in guava patch

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL/CLUMPED <1 TO 2-3M	EQUAL 3.8 M	CLUMPED 1 TO 3-4

Table 3.14 Guava patch characteristics presented as average number per 100 m^2

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25 TO 1.9 M	LIANAS
8.25 (RANGE 3 - 12)	62.2°F 83°F	6.2 (RANGE 0 – 11)	1.4 (RANGE 0 – 6)	1.6 (RANGE 0-3)	10.8 (RANGE 7 -14)

PLOT 700-750: This area was not an official point count patch. But because groups of *Eulemur* were observed to frequent this area, it was quantified as a means of comparison. If lemurs (or animals in general) are going to use the guava, they have to be able to move through this habitat type to access the adjacent patch. Only one plot was quantified in this area. The end of the guava thickets occurs between 700 and 750 meters. The guava then dissipates into isolated patches in the forest. The guava is still conspicuous here (73 plants/100 m^2), forming pockets throughout the patch. Ravinalas are prominent in this area (18/100 m^2) with an average height of 4.7 meters. This area has the highest density of ravinalas of the patches. There is an increase in non-guava 1-5 cm dbh trees (45/100 m^2) and non-guava 6-10 cm dbh trees (38/100 m^2). These trees are equally distributed and are often less than half a meter apart. This plot has one of the highest densities of 1-5 cm and 6-10 cm dbh trees. The connected canopy height is still relatively low in this area of around 3.8 to 4.7 meters. Larger (>21 cm) dbh trees are still sparse here and tend to be clumped rather than equally spaced.

The most common trees here are guava, voapaka keliravina, ravinala, tsipatika, and menahihy (Table 3.15). Voapaka are small to large trees distinguishable by their well-developed stilt roots. Tsipatika are also small to large trees but distinguished by their white exudate, while menahihy are shrubs to medium sized trees.

Trees of Economic and Ecological Value

Eighteen ravinalas (*Ravenala* sp.), two hazomafana (*Diospyros* sp.) trees, 73 guava trees, and one hazomainty (*Diospyros* sp.) tree were identified in a 100 m^2 area. No lemur taxa were observed to use the hazomafana trees, but as previously stated, this location was not an official point count patch. Similar to the guava, the ravinala palms in Patch 750 were important trees for the brown lemurs both for movement, resting, and as a food resource. The brown lemurs consumed the nectar, flowers, and seeds of the ravinala on a regular basis. The brown lemurs did not

preferentially use the guava in this patch for movement or resting even though it was available. Rather, the brown lemurs used a wide range of different substrates.

Table 3.15 Common trees found in 750 patch

PATCH	MALAGASY TREE	NUMBER IN PATCH	FAMILY	SPECIES
750	GUAVA	73	MYRTACEAE	*PSIDIUM CATTLEIANUM*
750	VOAPAKA KELIRAVINA	46	EUPHORBIACEAE	*UAPACA LOUVELLII*
750	RAVINALA	18	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
750	TSIPATIKA	14	MORACEAE	*STREBLUS SPP*
750	MENAHIHY	13	ANACARDIACEAE	*CAMPYLOSPERMUM SP*
750	LIANNE	11	?	*?*
750	VOAPAKA BERAVINA	6	EUPHORBIACEAE	*UAPACA AMPLIFOLIA*
750	TROVA BERAVINA	5	MORACEAE	*TRECULIN SP*
750	AMBONAMBONA	4	ARALIACEAE	*POLYSCIA SP*
750	HAZOMALANY	4	RHIZOPHORACEAE	*CASSIPOUREA SP*
750	MAKARANANA	4	EUPHORBIACEAE	*MACARANGA HISPIDA*
750	SADOKA BERAVINA	4	RUBIACEAE	*GAERTNERA SP*
750	TARANTANA	4	ANACARDIACEAE	*MICHRONYCHIA MACROPHILIA*
750	TAVOLO FOTSY	4	LAURACEAE	*CRYPTOCARYA SP*

PATCH 800-900: This area is in a transition zone from the degraded forest full of invasive guava to primary forest. Because this is a transition zone, the quantified plots demonstrate different characteristics with a variety of vegetative substrates. The first plot is located on a ridgeline (slope = 26 degrees). The most common trees here are tavolo fotsy, lalotina, and vongo be ravina (Table 3.16). Lianas are prominent (19/100 m^2) creating congestion in the understory and extending up to 3.8 meters blurring any vertical space.

The second plot is located on an incline of 32 degrees. This area is more congested with a higher density of ravinalas. The ravinala leaves are abundant, falling over and contributing to the continuous connected layer at a height of 4.7 to 5.6 meters. Abundant low-lying vegetation, multiple tree falls, and liana tangles monopolize a large component of this area. In this plot, trees with an 11-20 cm dbh are less dense and there is more low-lying herbaceous growth. The trees of

varying dbh tend to form clumped spatial patterns, (Table 3.20). There is one emergent 16 meter ramy tree in this plot that was used repeatedly by *Eulemur* as a sleeping site in this plot. The most abundant trees are lalotina and mampay (Table 3.16).

The third plot is east of the ridge in a small valley transitioning into primary forest. The lower 3.8 to 5.6 meter canopy layer is connected. The upper canopy averages between 9.4 and 12.5 meters with one emergent 16 meter tree. This taller layer is connected with small gaps. There are no ravinalas in this plot or in the immediate area. Of the three plots, this area has the greatest density of 11-20 cm dbh trees. The 6-10 cm and 11-20 cm dbh trees are equally distributed whereas the larger dbh trees tend to be more clumped. The common trees are mampay and makarana (Table 3.6).

Plot 4 is on a steeper slope (40 degrees). Ravinalas are prominent in addition to voapaka keliravina, lazalaza, and tarantana. There are several standing dead trees, abundant leaf litter, and 5 young guava trees. Further down the slope there is a patch of longoza that extends southwest to the edge of the reserve.

In all four plots the canopy cover is about 70%. One-5 cm dbh (30.5/100 m^2) and 6-10 dbh (15.8/100 m^2) are more abundant than larger dbh trees. The number of 21+ cm dbh trees has slightly increased (4.8/100 m^2) here relative to the other plots although the larger dbh trees are still primarily clumped ravinala palms. Emergent trees on average are 15.7 m (1/100 m^2). Overall, lalotona, mampay, ravinala, and voapaka keliravina are the most common trees (Table 3.16).

Trees of Economic and Ecological Value in Patch 800-900

There are several trees of economic and ecological value in this patch, including ten mampay (*Cynometra* sp.), seven hazomainty (*Diospyros* sp.), five hasina keilravina (*Dracaena* sp.), two azinina (*Symphonia* sp.), nineteen ravinalas (*Ravenala* sp.), five guava (*Psidium* sp.), and four ramy (*Canarium* sp.) trees. One emergent 16 meter ramy tree, in particular, has been utilized repeatedly by *Eulemur* groups as a sleeping site.

The main fruits the brown lemurs consumed in this patch were from the liana. I am unaware of any economic significance of these plants to humans. But, they are ecologically important to the brown lemurs. The mampay trees were not observed to flower over this study period and so the importance of those trees to lemurs remains unknown. Although, in other parts of the forest where mampay trees were in bloom, various lemur taxa actively foraged for consumed the flowers in large quantities. The brown lemurs used ravinala and palm leaves as the chosen substrates to move along, especially where these substrates formed continuous highways through the canopy for the lemurs.

There is also one molanga (*Dombeya* sp.) and one antafara (*Petchia* sp.) tree in the patch indicators of past disturbance, as these trees tend to colonize open, light gap areas.

Table 3.16 Common trees found in Patch 800-900

PATCH	MALAGASY TREE	NUMBER	FAMILY	SPECIES
800-900	GUAVA	5	MYRTACEAE	*PSIDIUM CATTLEIANUM*
800-900	HASINA KELIRAVINA	5	CONVALLARIACEAE	*DRACAENA REFLEXA*
800-900	LIANNE	41	?	*?*
800-900	HAZOMAINTY	7	EBENACEAE	*DIOSPYROS SP*
800-900	LALOTONA	15	EUPHORBIACEAE	*ANTHOSTEMA MADAGASCARIENSIS*
800-900	LAZALAZA	5	EUPHORBIACEAE	*CROTON NOBILIS*
800-900	MAKARANANA	10	EUPHORBIACEAE	*MACARANGA HISPIDA*
800-900	MAMPAY	10	FABACEAE	*CYNOMETRA SPP*
800-900	RARA	7	MYRISTICACEAE	*BRONCHONEURA SP*
800-900	RAVINALA	19	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
800-900	SADOKA KELIRAVINA	9	RUBIACEAE	*GAERTNERA SP*
800-900	TARANTANA	6	ANACARDIACEAE	*MICHRONYCHIA MACROPHILIA*
800-900	TAVOLO FOTSY	11	LAURACEAE	*CRYPTOCARYA SP*
800-900	TSIPATIKA	5	MORACEAE	*STREBLUS SPP*
800-900	VOAPAKA KELIRAVINA	13	EUPHORBIACEAE	*UAPACA LOUVELLII*
800-900	VONGO BE RAVINA	5	CLUSIACEAE	*RHEEDIA SPP*

Temperature/Humidity in Patch 800-900

At 800/900 meters the temperature ranged from 64.4°F to 83°F with the hottest temperatures in October and November (Table 3.17). The lowest temperatures occurred in October (65°F). The humidity remained fairly constant June to November from 66% to 95.5%. Patch 800-900 has the lowest average temperatures of any of the patches.

Table 3.17 Averages of daily temperature and humidity fluctuations in Patch Guava

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	91.3%	85.7%	83.7%
TEMPERATURE AVERAGE	67.8°F	72.4°F	72.2°F

800-900 Patch Comparison

This transitional zone exhibits different characteristics among the plots with a variety of vegetative substrates. The density of 1-5 cm and 6-10 cm dbh trees are on the higher end of the spectrum in comparison to the density of these trees in other patches (Tables 3.9, 3.17). The density of 11 – 20 cm and 21+ cm dbh are not as abundant as the smaller dbh trees in this patch and in comparison to the other patches; the number of larger dbh trees is also less overall in patch 800-900 (Table 3.18).

Table 3.18 Average number of varying dbh trees within 100 m² in the 800-900 patch.

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
30.5 (RANGE 25 – 36)	15.8 (RANGE 8- 22)	5.3 (RANGE 3 - 8)	4.8 (RANGE 2 – 7)

Canopy connectedness varied. The first canopy layer is mainly connected, the second layer has areas of connectedness and small gaps, while the third layer has small and/or connected gaps in areas, medium and/or large gaps in others, and even in-between areas of small/medium gaps. This level of variability is due to the transitional nature of forest types that this patch represents.

The heights of the first, second, and third canopy layers are at the lower end of the spectrum

relative to other patches (Table 3.19). There are also occasional emergent trees at a height of 15.6 m. This emergent height is one of the shorter emergent heights in comparison to the other patch height characteristics (Table 3.19).

The 6-10 cm dbh trees are equally spaced at about 1 meter. The 11-20 cm dbh trees are either clumped or equally spaced (Table 3.20). This is one of two patches (the other is Patch Zubenubi) that contain this type of spatial distribution of 11-20 cm dbh trees. The 21+ cm dbh trees are clumped, which is consistent with the pattern shown in other patches.

Table 3.19 Average canopy heights in 800-900 patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	EMERGENT TREE HEIGHT
4.1 M (RANGE 1.9 – 5.6)	7.4 M (RANGE 6.3 – 8.1)	11.0 M (RANGE 8.1 – 13.2)	15.6 M

The number of ravinala palms is variable with some areas containing no palms and other areas containing up to 10 palms within a 100 m^2 area. The total number (N=19) of ravinalas is higher compared to the other patches and the density of ravinala palms is greater in comparison to other attributes within the patch (Table 3.21). The average height of the ravinalas (6.5 m, range 3.8 – 9.4 m) is lower compared to the other patches. There is also some guava growing in this area but this invasive tree is very sparse here in comparison to the thickets found further south in the reserve. There is also a high count of standing and fallen dead (Table 3.8).

Table 3.20 Spatial distributions of trees of varying dbh in 800-900 patch

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL 1 M	EQUAL/CLUMPED 2 TO 3 M	CLUMPED 1 TO 6 M

Table 3.21 800-900 patch characteristics presented as average number per 100 m²

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25 -1.9 M	LIANAS	STANDING DEAD TREES	FALLEN DEAD TREES	PALMS
4.8 (RANGE 0 – 10)	64.4°F 83.0°F	5.1 (RANGE 1-10)	0.8 (RANGE 0-2)	1.0 (RANGE 0-1)	10.3 (RANGE 6-19)	2.3 (RANGE 0-4)	3.8 (RANGE 1-6)	4.0 (RANGE 3-5)

PATCH 1600: The plots for patch 1600 were established 1600 meters inside the reserve. There is consistent 94.5% canopy cover in this area. One-5 cm dbh trees are quite abundant (42.8/100 m²) with fewer 6-10 cm (8/100 m²) and 11-20 cm (8/100 m²) dbh. Trees with 21+ cm dbh are rare (3/100 m²). The vertical space is cluttered due to the abundance of lianas and low-lying vegetation. Lianas are abundant (25/100 m²), contributing to even greater density of smaller dbh substrates (dbh range of 1-7 cm). Lianas clutter the ground and understory and extend up to 6.9 meters, becoming quite dense in some areas. There are major liana tangles in the northern portion of this patch before a steep vertical climb in the landscape.

The lower canopy is connected and has an average height of 7.8 meters extending up to a 9.4 meter layer of small gaps. The lianas fill all levels of canopy. There are six fallen rotting trees in this area that collect abundant dead branches and leaf litter. The brown lemurs specifically used the liana tangles as bridges to negotiate gaps in the canopy as well as to rest and eat its fruits.

There are three canopy levels. The first layer is connected with an average height of 5.2 meters, the second is connected with some small gaps and an average height of 9.4 meters, and the third is approximately 14 meters tall with medium gaps in the canopy. Emergent trees contribute to the patch complexity (1.3/100 m²). There is no guava growth and ravinala palms are rare (0.5/100 m²) (N=2). The slope is variable and ranges from 9 degrees on the ridge to 40 degrees on the slope. The most common plants include hasina keliravina, sadoka keliravina, tavolo fotsy, and azinina (Table 3.22).

Trees of Economic and Ecological Value in Patch 1600

Three ramy (*Canarium* sp.), one mampay (*Cynometra* sp.), two ravinala (*Ravenala* sp.), and 18 hasina (*Dracaena* sp.) trees were counted in this patch, trees with economic value to humans as well as ecological value to the lemurs. Hasina is the most abundant plant, secondary to liannas. Brown lemurs frequently used the canopy of these hasina trees to move through this patch. Sifaka were also observed to use the trunks of the hasina tree to move through this patch in addition to eating its flowers. *Eulemur* groups commonly ate fruit from two zanamena (*Dialium unifoliolatum*) trees. Zanamena fruits are also consumed by people. Two afomena (*Dombeya* sp.) trees were counted in this patch perhaps indicators of past disturbance.

Table 3.22 Common trees found in patch 1600

PATCH	MALAGASY TREE	NUMBER	FAMILY	SPECIES
1600	AZININA	7	CLUSIACEAE	*SYMPHONIA SP*
1600	FAHAVALOTRAZO	6	RUTACEAE	*ZANTHOXYLUM SP*
1600	GUAVA	0	MYRTACEAE	*PSIDIUM CATTLEIANUM*
1600	HASINA KELIRAVINA	18	CONVALLARIACEAE	*DRACAENA REFLEXA*
1600	LAZALAZA	5	EUPHORBIACEAE	*CROTON NOBILIS*
1600	OMPA	6	?	
1600	RARA	6	MYRISTICACEAE	*BRONCHONEURA SP*
1600	RAVINALA	2	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
1600	LIANNE	100	?	*?*
1600	SADOKA KELIRAVINA	10	RUBIACEAE	*GAERTNERA SP*
1600	SOMOTRONANA	5	SAPINDACEAE	*STADMANIA SP*
1600	TAVOLO FOTSY	11	LAURACEAE	*CRYPTOCARYA SP*
1600	TAVOLO MENA	5	LAURACEAE	*CRYPTOCARYA SP*
1600	TELOTRITRY	6	RHAMNACEAE	*BATHIORHAMNUS LOUVELII*
1600	VOAPAKA BERAVINA	5	EUPHORBIACEAE	*UAPCA AMPLIFOLIA*

Temperature/Humidity in Patch 1600: At 1600 meters the temperature ranged from the mid 60s to 70.8 degrees Fahrenheit with the hottest temperatures in June, October, and November (Table 3.23). The lowest temperatures occurred in August and September. The humidity remained a fairly constant average of 95% June through November.

Table 3.23 Averages of daily temperature and humidity fluctuations in Patch 1600

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	96.2%	95.6%	94.5%
TEMPERATURE AVERAGE	64.4°F	66.3°F	66.0°F

1600 Patch Comparison

Patch 1600 is distinctive in its high density of equally spaced 1-5 cm dbh trees. This patch has the highest number on average per 100 m^2 (Table 3.24). In contrast, this area has one of the lowest densities of 6 to 10 cm dbh trees (Table 3.24). The average number of 11-20 cm dbh trees is relatively high while that of 21+ cm dbh trees is relatively low (Table 3.24). The larger dbh trees tend to be clumped and more widely dispersed (Table 3.26).

Table 3.24 Average number of varying dbh trees within 100 m^2 in the 1600 patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
42.8 (RANGE 26 – 63)	8 (RANGE 6 – 9)	7.5 (RANGE 6 – 11)	3 (RANGE 1 – 5)

The first canopy layer is connected, the second layer is connected with some small gaps, and the third layer has medium gaps similar to the other patches. The first, second, and third canopy heights are some of the taller heights at these layers compared to other patch layers (Table 3.25). There are also fairly abundant emergent trees reaching heights at the taller end of the spectrum (Table 3.25). Trees of varying dbh are equally distributed (Table 3.26). Ravinalas are very rare (N=2) and there is no guava growth or bamboo in this patch (Table 3.27).

Table 3.25 Average canopy heights in 1600 patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	EMERGENT TREE HEIGHT
5.2 M (RANGE 3.8 – 6.3)	9.4 M (RANGE 8.5 – 10.7)	14 M (RANGE 12.5 – 15)	15.7 M (RANGE 15.6-16.3)

Table 3.26 Spatial distributions of trees of varying dbh in 1600 patch

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL 1 METER	EQUAL 1 TO 2-3 METERS	EQUAL 2 TO 4-5 METERS

There is a moderate total count (N=156) of new vegetation growth (Table 3.9). There is also one of the higher average densities of lianas (Table 3.26). In contrast, there is a low density of standing dead trees and fallen dead trees.

Table 3.27 1600 patch characteristics presented as average number per 100 m^2

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25-1.9 M	LIANAS	FALLEN DEAD TREES	PALMS
0.5 (RANGE 0 – 1)	63.0°F 70.8°F	13.3 (RANGE 3 - 32	2.0 (RANGE 1 – 5)	2 (RANGE 1 – 3)	25.0 (RANGE 16 -34)	0.25 (RANGE 0-1)	0.75 (RANGE 0 -1)

PATCH SAHABEFOZA: Sahabefoza is an interesting patch in that the adjacent area consists of a large expanse of longoza (Family Zinziberaceae, *Afromomum angustifolium*). The longoza field is approximately 30 meters wide and 700 meters long. The longoza continues to the west down a very steep slope until it ends at the river's edge of the Ivoloina River. In the distance from the patch there are several 21.9 meter trees growing on the periphery of the longoza field. There are also two smaller 169 m^2 areas of longoza in the point count area. One longoza area grows on the slope and the other farther down in the valley.

Longoza is a cardamom plant that is evidence of past agricultural encroachment inside of the reserve. This plant colonizes open gaps in the forest and can be found growing in varying sized patches to just a few single plants growing randomly throughout the forest. Longoza grows up to 2.5 meters tall and there can be as many as 10 stalks in one square meter. Mazomboty, another colonizing, but viney plant, is often packed in and around the longoza creating a very dense wall of

vegetation. Bush pigs (*Potamochoerus* sp.) generate tunnels throughout the longoza creating both space for themselves to move and to wallow in the mud, as well as space for humans to move through an otherwise impenetrable vegetative wall.

The area before (south) the large expanse of longoza has abundant liana and vines clustered around a tree fall that extend up to the 6.3 meter layer and ensconce several trees and compacted dead vines. The 3.8 meter layer is connected and congested due to the density of 1-5 cm dbh (53/100 m^2) trees and lianas (42/100 m^2). The 6.3 meter and 9.4 to 10.9 meter layers are connected with some small gaps due to tree falls. The point count vegetation patch is located on the northern edge of the longoza and extends further north ending right before a small river. The slope varies from a steep 36 degrees to 5 degrees as one approaches the river, which is then again followed by a steep incline. Canopy cover averages between 55 and 70%.

One-5 cm dbh (21.5/100 m^2) and 6-10 cm dbh (14.3/100 m^2) trees are common with 11-20 cm dbh (4/100 m^2) and 21+ cm (2.5/100 m^2) dbh trees more scarcely distributed. Ravinala palms account for the larger dbh trees (2.3/100 m^2). There are three main canopy levels with the occasional 15.6 meter emergent tree (1/100 m^2). Layers one (3.5 meters) and two (7.5 meters) are connected and level three (9.9 – 11.4 meters) has medium gaps throughout the canopy. The vegetation on the slope is much denser with no clear vertical space at 5 meters. The valley area is more open with fewer small dbh trees.

New guava plants are invading this patch with several thick stands (21/100 m^2). Palms such as apanga and pandanus are abundant in patches (9/100 m^2 and 14/100 m^2). Pandanus (*Pandanus* sp.) is a shrub to large sized tree with long narrow leaves with spines along the margins. The most common tree species are the invasive guava, gavola, menahihy, and sadoka keliravina (Table 3.28). Sahabefoza has one of the highest counts of new plant (0-2 meters) growth (N=304) (Table 3.27).

Trees of Economic and Ecological Value in Patch Sahabefoza

One ramy (*Canarium* sp.), molanga (*Dombeya* sp.), and mampay (*Cynometra* sp.) tree and two hasina (*Dracaena* sp.), four ravinala (*Ravenala* sp.), and thirty guava (*Psidium* sp.) trees were counted. The brown lemurs were observed to eat from, rest, and move in two primary famelona (*Chrysophyllum* sp.) trees. The brown lemurs also frequently rested in a molanga tree (*Dombeya* sp.) in the valley region of this patch. Thirty guava (*Psidium catteianum*) plants were counted. The guava was not in bloom over the time period of this research and so the importance of the guava fruits to the lemurs could not be evaluated.

Table 3.28 Common trees found in Patch Sahabefoza

PATCH	MALAGASY TREE	NUMBER IN PATCH	FAMILY	SPECIES
SAHABEFOZA	AMBONAMBONA	6	ARALIACEAE	*POLYSCIAS SP*
SAHABEFOZA	AMBORASAHA	8	MENISPERMACEAE	*BURASAIA GRACILIS*
SAHABEFOZA	GAVOLA	20	MYRTACEAE	*EUGENIA SP*
SAHABEFOZA	GUAVA	30	MYRTACEAE	*PSIDIUM CATTLEIANUM*
SAHABEFOZA	HAZOAMBO	5	ANNONACEAE	*XYLOPIAS SPP*
SAHABEFOZA	MENAHIHY	19	ANACARDIACEAE	*CAMPYLOSPERMUM SP*
SAHABEFOZA	RARA	3	MYRISTICACEAE	*BRONCHONEURA SP*
SAHABEFOZA	RAVINALA	9	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
SAHABEFOZA	SADOKA KELIRAVINA	11	RUBIACEAE	*GAERTNERA SP*
SAHABEFOZA	SOMOTRONANA	8	SAPINDACEAE	*STADMANIA SP*
SAHABEFOZA	TARANTANA	9	ANACARDIACEAE	*MICHRONYCHIA MACROPHILIA*
SAHABEFOZA	TAVOLO FOTSY	3	LAURACEAE	*CRYPTOCARYA SP*
SAHABEFOZA	TSIPATIKA	5	MORACEAE	*STREBLUS SPP*

Temperature/Humidity in Patch Sahabefoza

At Sahabefoza humidity was a fairly consistent percentage throughout this research with the highest percentages occurring in the morning and then tapering off as the day progressed (Table 3.29). The average temperature was often the highest in mid afternoon (Table 3.29).

Sahabefoza experienced the highest temperatures in the month of June (69.2°F – 75.0°F) and the coldest temperatures during July and August (65.3°F – 64.0°F).

Table 3.29 Averages of daily temperature and humidity fluctuations in Patch Sahabefoza

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	92.8%	86.9%	87.8%
TEMPERATURE AVERAGE	68.2°F	70.7°F	70.4°F

Sahabefoza Patch Comparison

Of all the patches Sahabefoza has the greatest density and closest proximity to an extensive field of longoza. It is also the only patch in close proximity to a small river that runs through the northern portion. Invasive guava grows in pockets at varying densities from zero plants up to 21 plants per 100 m^2 throughout this patch. The guava here is not as thick as the guava found in the southern portion of BNR but is more abundant than the new guava growth farther north in Patch Sahakoho for instance. The slope in this patch is also variable ranging from 36 degree inclines to a 5 degree relatively flat valley landscape.

Relative to the other patches, Sahabefoza has a lower density of 1-5 cm, 11-20 cm, and 21+ cm dbh trees and a higher density of 6 -10 cm dbh trees within the patch (Table 3.30). The smaller dbh trees have an equal spatial distribution whereas the larger dbh trees tend to be more clumped (Table 3.32).

The canopy is connected in both layers one and two followed by an abrupt leap to medium gaps among the taller trees. Patch Sahabefoza has one of the shortest first layer canopy heights (along with patch guava) as well as the second and third layer canopy heights (Table 3.31). The occasional emergent trees are also shorter than emergent trees found in other patches (Table 3.31).

Table 3.30 Average number of varying dbh trees within 100 m² in the Sahabefoza patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
21.5 (RANGE 14 – 35)	14.3 (RANGE 10 – 19)	4.0 (RANGE 3 – 7)	2.5 (RANGE 1 – 4)

Table 3.31 Average canopy heights in Sahabefoza patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	EMERGENT TREE HEIGHT
3.5 M (RANGE 1.3 – 5.0)	7.4 M (RANGE 4.9 – 9.9)	11.4 M (RANGE 9.0 – 13.8)	14.1 M (RANGE 12.5 – 15.6)

Table 3.32 Spatial distributions of trees of varying dbh in 1600 patch

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL 1 METER	EQUAL 1 TO 2 METERS	CLUMPED 2 TO 7 METERS

The average number of ravinala palms per 100 m², and even more so, the number of apanga/pandanus palms is relatively high (Table 3.33). The amount of herbaceous ground cover is quite dense but the taller new growth treelets are sparse (Table 3.33).

Table 3.33 Sahabefoza patch characteristics presented as average number per 100 m²

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25-1.9M	LIANAS	STANDING DEAD TREES	FALLEN DEAD TREES	PALMS
2.3 (RANGE 1-5)	64.0°F 75.0°F	6.8 (RANGE 1- 15)	0.5 (RANGE 0 – 2)	0.8 (RANGE 0 – 3)	21 (RANGE 14 - 29	0.5 (RANGE 0 – 2)	0.8 (RANGE 0 – 1)	1.6 (RANGE 1 – 14)

PATCH FARA: The Fara point count area is located in a valley with a relatively flat slope (5 to 22 degrees) and near a small stream. There are four canopy layers. The lower 4.8 – 5.6 meter canopy has small gaps and is not continuous. There are fewer 1-5 cm dbh (26.5/100 m²) and 6-10 cm dbh (5.5/100 m²) trees in Fara creating a less dense understory, allowing for more vertical space at lower levels. The 6-10 cm dbh trees are spatially clumped (<1 to 2-3 meters apart) whereas the 11-

20 cm dbh trees are more equally spaced (1 to 2 meters apart) (Table 3.38). Eleven-20 cm dbh (8.8/100 m^2) trees are prominent and consistent. There are several trees with a dbh greater than 50 cm. Canopy levels two (7.8 – 10.0 meters) and three (15.2 – 15.6 meters) are continuous and also form the main layers. The fourth layer (19.7 – 20.3 meters) has medium and large gaps within the canopy. Emergent trees are found here (1/100 m^2) ranging in height between 26.3 and 31.3 meters. The canopy cover ranges from 56.3% to 87.5%. New vegetation growth is prominent (N=329) while the lianas are less abundant (N=66).

The most common trees in Fara are azinina and antafara (Table 3.34). Nine giant bamboo stalks were also counted in this area. There is no guava. Adjacent to plot 4, there is an increase in liana (30/100 m^2) that extends up to the 6.3 meter layer. The lower 2 - 3.8 meter layer is more connected compared to the other areas of Fara. The 6.3 meter layer is connected and the 9.4 meter layer has small and medium gaps. The 6-10 cm dbh trees in this area are more equally spaced along with the 11-20 cm dbh and 21+ cm dbh trees. There is also a small area of longoza 4 m^2, abutting this plot.

Trees of Economic and Ecological Value in Patch Fara

One ramy (*Canarium* sp.) and zanamena (*Dialium* sp.*)* tree plus eleven azinina (*Symphonia* sp.), 67 hasina (*Dracaena* sp.), seven hazomainty (*Diospyros* sp.), and five mampay (*Cynometra* sp.) trees were counted. Here, the lemurs were either moving or resting, but not feeding. Hasina is the most abundant tree taxon and was frequently used by the lemurs for movement.

Table 3.34 Common trees found in patch Fara

PATCH	MALAGASY TREE	NUMBER	FAMILY	SPECIES
FARA	AMBORASAHA	6	MENISPERMACEAE	*BURASAIA GRACILIS*
FARA	ANTAFARA	11	APOCYNACEAE	*PETCHIA SP*
FARA	AZININA	11	CLUSIACEAE	*SYMPHONIA SP*
FARA	GUAVA	0	MYRTACEAE	*PSIDIUM CATTLEIANUM*
FARA	HASINA KELIRAVINA	67	CONVALLARIACEAE	*DRACAENA REFLEXA*
FARA	LIANNE	66	?	*?*

FARA	HAZOMAINTY	7	EBENACEAE	*DIOSPYROS SP*
FARA	HAZONDOMOINA	4	EUPHORBIACEAE	*TANNODIA SP*
FARA	MAMPAY	5	FABACEAE	*CYNOMETRA SPP*
FARA	RARA	4	MYRISTICACEAE	*BRONCHONEURA SP*
FARA	RAVINALA	0	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
FARA	SADOKA BERAVINA	4	RUBIACEAE	*GAERTNERA SP*
FARA	TAVOLO FOTSY	10	LAURACEAE	*CRYPTOCARYA SP*
FARA	VOAPAKA KELIRAVINA	4	CLUSIACEAE	*UAPACA LOUVELLII*
FARA	VONGO BERAVINA	4	CLUSIACEAE	*RHEEDIA SPP*

Temperature/Humidity in Patch Fara: At Fara, the temperature ranged from the low 60s to 80 degrees Fahrenheit with the hottest temperatures in June (72.5°F) and November (80.0°F) (Table 3.35). The lower temperatures occurred in July (62.3°F) and August (63.2°F). The humidity ranged from 86% to 100% with the highest percentage of humidity recorded in the mornings (Table 3.35).

Table 3.35 Averages of daily temperature and humidity fluctuations in Patch Fara

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	95.5%	91.3%	90.7%
TEMPERATURE AVERAGE	66.0°F	68.5°F	68.6°F

Fara Patch Comparison

Fara is a less undulating patch (slope range 5° to 22°) itself situated between very steep inclines (42°) in all directions. Fara is rather eclectic in that giant bamboo grows in patches here, there is a small stream running through the northern portion of the patch that is adjacent to a 4 m^2 area of longoza, and the tallest emergent trees grow here. There is a moderate density of 1-5 cm and 21+ cm dbh trees and the lowest density of 6-10 cm dbh trees compared to these same densities in other patches. This patch has one of the highest densities of 11-20 cm dbh trees (the other being Patch Sahakoho) (Table 3.36). The sparse 6-10 cm dbh trees are spatially clumped at 1 to 3-4 meters while the 11-20 cm dbh trees are equally distributed much closer at one meter apart. The larger dbh trees are also clumped at 1 to 4-5 meters (Table 3.38).

Table 3.36 Average number of varying dbh trees within 100 m^2 in the Fara patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
26.5 (RANGE 21 – 32)	5.5 (RANGE 5 -7)	8.8 (RANGE 6 – 10)	3.8 (RANGE 2 – 6)

Only Patch Fara has small gaps as well as areas of connectedness in canopy layer one, while layers two and three are both connected. It is also the only patch to have a consistent fourth layer with medium/large gaps. Canopy heights one and two are in the middle of the range in comparison to the other patches while the third canopy height is relatively higher (Table 3.37). The tallest emergent trees grow here (Table 3.37).

Table 3.37 Average canopy heights in Fara patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	CANOPY HEIGHT LAYER 4	EMERGENT TREE HEIGHT
4.0 M (RANGE 2.2 – 7.8)	7.8 M (RANGE 8.1 – 10.1)	15.0 M (RANGE 14.1 – 16.1)	19.7 M (RANGE 19.1 – 20.3)	31.3 M (N =1)

Table 3.38 Spatial distribution of trees of varying dbh in Patch Fara

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
CLUMPED 1 TO 3-4 METERS	EQUAL 1 METER	CLUMPED 1 TO 4-5 METERS

There are no ravinala palms and the density of other palm species is also low. Fara has one of highest densities of herbaceous new growth (Table 3.39). There are no dead or fallen trees. The density of lianas is towards the lower end of the spectrum.

Table 3.39 Fara patch characteristics presented as average number per 100 m²

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25-1.9M	LIANAS	STANDING DEAD TREES	FALLEN DEAD TREES	PALMS
0	60°F 80°F	13.6 (RANGE 3 – 30)	1.3 (RANGE 1 – 3)	0.7 (RANGE 0 – 1)	16.5 (RANGE 5 – 30)	0	0	2 (RANGE 1 – 2)

PATCH BETAKONONA: Betakonona is located on a ridge (slope = 5 degrees) with a steep sloping landscape on either side (slope= 36 degrees). This area of the forest was often covered in low clouds and quite windy. The terrain in this area of the forest is extremely undulant and steep. The Ivoloina River flows in a valley east and south of this patch. The river can be heard while standing in Patch Betakonona. There are three main canopy layers. The lower canopy (4.6 meters) is connected with some small gaps. The second level is the main continuous level at an average height of 8.7 meters. The third, 17.8 – 18.8 meter layer, has small and medium gaps within the canopy.

The average canopy cover is 77.4%. Spacing between tree trunks was contingent on whether they were located on the ridgeline or farther down the slope. On the ridge, 11-20 cm dbh (6.8/100 m²) trees are more equally spaced at <1 to 1 meter apart. On the slope they have more of a clumped distribution (<1 to 2-2.5 meters). The 6-10 cm dbh (12.5/100 m²) trees are equally spaced throughout the patch although they are a bit more abundant on the slope, 19/100 m², compared to 8/100 m² on the ridge. The 11-20 cm dbh trees are prevalent numbering up to 10/100 m² as are the 21+ cm dbh trees. The 21+ cm dbh trees have a clumped distribution on the slope of 1 to 3-4 meters and an equal distribution on the ridge of 2 to 3 meters. There are several trees that have large dbh's of 52 cm and 64 cm in this area as well. There are no guava trees or ravinala palms. However palms such as apanga and pandanus are abundant in pockets 9/100 m². The most common tree is vongo keliravina (Table 3.40).

Trees of Economic and Ecological Value in Patch Betakonona

One afomena (*Dombeya* sp.) and zanamena (*Dialium* sp.) tree plus six azinina (*Symphonia* sp.), four hazomainty (*Diospyros* sp.), six mampay (*Cynometra* sp.), and seven ramy (*Canarium* sp.) trees were counted in this patch. All of the lemur taxa observed in this patch ate the young leaves of the mampay trees.

Table 3.40 Common trees found in patch Betakonona

PATCH	MALAGASY TREE	NUMBER	FAMILY	SPECIES
BETAKONONA	ANTAFARA	13	APOCYNACEAE	*PETCHIA SP*
BETAKONONA	AZININA	12	CLUSIACEAE	*SYMPHONIA SP*
BETAKONONA	GUAVA	0	MYRTACEAE	*PSIDIUM CATTLEIANUM*
BETAKONONA	HAZOMAINTY	4	EBENACEAE	*DIOSPYROS SP*
BETAKONONA	HAZONDOMOINA	13	EUPHORBIACEAE	*TANNODIA SP*
BETAKONONA	MAMPAY	6	FABACEAE	*CYNOMETRA SPP*
BETAKONONA	RAMY	7	BURSERACEAE	*CANARIUM MADAGASCARIENSIS*
BETAKONONA	RARA	9	MYRISTICACEAE	*BRONCHONEURA SP*
BETAKONONA	RAVINALA	0	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
BETAKONONA	TSIPATIKA	4	MORACEAE	*STREBLUS SPP*
BETAKONONA	VADIOANDRO	5	?	*?*
BETAKONONA	VONGO KELIRAVINA	70	CLUSIACEAE	*RHEEDIA SPP*

Temperature/Humidity in Patch Betakonona: At Betakonona the humidity ranged from 87% in June to 94.8% in August and 95.5% in September (Table 3.41). The hottest temperatures were in June (67°F), October (71°F), and November (71°F). The coolest temperatures were in August and September at around 63°F.

Table 3.41 Averages of daily temperature and humidity fluctuations in Patch Betakonona

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	90.8%	91.5%	88.1%
TEMPERATURE AVERAGE	68.1°F	67.8°F	67.8°F

Betakonona Patch Comparison

Although the average temperature was 63°F, this patch always felt colder than the other patches due to a fairly consistent low cloud cover and frequent wind gusts. The terrain in this area of the forest is extremely undulant and steep with the Ivoloina River flowing through the valley to the east and south of this patch**.**

One of the highest densities of 1-5 cm dbh trees occurs in this patch (the other patches being, Guava and 1600) (Table 3.42). The densities of 6-10 cm and 11-20 cm dbh trees fall within the medium range while larger 21+ cm dbh trees are more prevalent. The smaller dbh trees are equally distributed at ≤ 1meter. The close proximity of the 6-10 cm dbh trees is a characteristic observed in only half of the quantified patches. The larger dbh trees tend to be more clumped which is a common pattern also observed throughout the other patches (Table 3.44).

Table 3.42 Average number of varying dbh trees within 100 m^2 in the Betakonona patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
33.0 (RANGE 20 – 40)	12.5 (RANGE 8 – 19)	6.8 (RANGE 5 – 10)	6.8 (RANGE 4 – 10)

Canopy heights one and two are in the medium height range in comparison to these canopy levels in other patches (Table 3.43). The canopy height for layer three is the tallest height at this level and there are no emergent trees. Canopy heights one and two are connected while the third canopy layer has small to medium gaps. Betakonona is the only patch where this canopy connectedness pattern is observed.

Table 3.43 Average canopy heights in Betakonona patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	EMERGENT TREE HEIGHT
4.6 M (RANGE 3.2 – 5.6)	8.7 M (RANGE 6.3 – 10.9)	17.8 M (RANGE 15.6 – 20.2)	NO EMERGENTS

Table 3.44 Spatial distribution of trees of varying dbh

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL <1 M	EQUAL 1 M	CLUMPED 1 TO 3-4 M

There are no ravinala palms, but there is a relatively high density of other palm species (Table 3.45). The lower lying herbaceous new growth is low-to-moderate here while taller new growth and treelets are prevalent. But, from a within patch comparison the low level herbs are more prevalent than the taller new growth. The densities of liana, dead standing, and dead fallen trees are moderate in comparison to other patches (Table 3.45).

Table 3.45 Betakonona patch characteristics presented as average number per 100 m^2

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25-1.9M	LIANAS	STANDING DEAD TREES	FALLEN DEAD TREES	PALMS
0	63°F 71° F	6.1 (RANGE 1 - 12)	0.8 (RANGE 0 - 2)	1.1 (RANGE 0 – 3)	18.5 (RANGE 6 – 27)	0.8 (RANGE 0 -2)	0.8 (RANGE 0 – 2)	3.3 (RANGE 0 – 9)

PATCH ZUBENUBI: The lianas form tangles at all levels and angles creating essentially one closed prominent canopy layer starting from the ground and extending up to 6.3 – 7.5 meters, masking much of the vertical space. On average, 110 lianas were counted per 100 m^2 although in some areas the number of lianas was as high as 158/100 m^2. The second canopy layer averages at 9.2 meters with small gaps throughout while the third 12.3 meter layer is inconsistent with wider medium gaps. There are the occasional 17.5 – 20.3 meter emergent trees in the surrounding area.

The majority of the smaller dbh substrates are due to the liana tangles, although 1-5 cm dbh (12.8/100 m^2) and 6-10 cm dbh (13.8/100 m^2) trees are found here. One-5 cm dbh trees have the lowest total count (N=51). There is spatial tree abundance variation pertaining to the 6-10 cm dbh trees. In some areas the 6-10 cm dbh trees have a density of 7/100 m^2 while in other areas the density reaches 26/100 m^2. In either density, these trees tend to be equally distributed at <1 to 1 meter. Eleven to 20 cm dbh trees (5.3/100 m^2) are both clumped and equally distributed at 1 to 2

meters. The 21+ cm dbh trees have on average a 30 cm dbh with the largest dbh measured to be 64 cm. These dbh trees are equally distributed at about three meters. The most common trees include ovobola, vintanona, antaijara, nofonakoho, vongo be ravina, mampay, and famelona (Table 3.46). Fallen trees (5/100 m^2) and dead trees (1/100 m^2) are common is this area and represent one of the highest counts (N=21) (Table 3.8).

A plot adjacent to the Zubenubi patch was also quantified for substrate comparison. This was done in order to assess further variation among lemur taxa that do or do not utilize patch Zubenubi. This adjacent area has an overall increase in canopy height as well as an increased number of larger dbh trees. There are three canopy levels. Level one (6 meters) is connected whereas levels two (9.2 meters) and three (12.3 meters) have small gaps that are connected in parts. Canopy cover is 70.1%. Liana abundance decreases here (64/100 m^2). Perhaps due to the decrease in liana, there are more equally spaced 1-5 cm dbh (20/100 m^2) and 6-10 cm dbh (19/100 m^2) trees in this area. The 11-20 cm dbh (4/100 m^2) and 21+ cm dbh (12/100 m^2) trees are spatially clumped at 1 to 2-3 meters. This area also has an increase in plant composition diversity.

Trees of Economic and Ecological Value

Ten mampay (*Cynometra* sp.), twenty five hazomainty (*Diospyros* sp.), six hasina (*Dracaena* sp.), and four azinina (*Symphonia* sp.) trees were counted in this patch. Thirteen afomena (*Dombeya* sp.) and five molanga (*Dombeya* sp.) shrubs and small trees were also counted here. This vegetation is often found in degraded open areas, secondary forests, and grow in light gaps in primary forest. The indri primarily focused on the young mampay leaves in taller trees growing on the periphery. Brown lemurs primarily ate liana fruits as well as fruit from the hasina trees. Given that hazomainty trees were prevalent these trees were important substrates for movement within and around this patch.

Table 3.46 Common plants in patch Zubenubi

PATCH	MALAGASY NAME	NUMBER	FAMILY	SPECIES
ZUBENUBI	HAZOMAINTY KELIRAVINA	19	EBENACEAE	*DIPSPYROS HAPLOSTYLIS*
ZUBENUBI	RARA	18	MYRISTICACEAE	*BRONCHONEURA SP*
ZUBENUBI	TROVA KELIRAVINA	14	MORACEAE	*TRECULIA SP*
ZUBENUBI	AFOMENA	13	MALVACEAE	*DOMBEYA SP*
ZUBENUBI	HAZONTOHO	12	MYRSINACEAE	*ONCOSTEMUM SP*
ZUBENUBI	TAVOLO FOTSY	12	LAURACEAE	*CRYPTOCARYA SP*
ZUBENUBI	SOMOTRORANA	11	SAPINDACEAE	*STADMANIA SP*
ZUBENUBI	MAMPAY	10	FABACEAE	*CYNOMETRA SPP*
ZUBENUBI	TSIMAMASALSOKONA	10	MELASTOMATACEAE	*MEMECYLON SPP*
ZUBENUBI	VONGO BERAVINA	9	CLUSIACEAE	*RHEEDIA SP*
ZUBENUBI	RAVINALA	1	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
ZUBENUBI	GUAVA	0	MYRTACEAE	*PSIDIUM CATTLEIANUM*
ZUBENUBI	MAROANDRO	8	EUPHORBIACAE	*BLOTIA SP*
ZUBENUBI	FAMELONA	6	SAPOTACEAE	*CHRYSOPHYLLUM SP*
ZUBENUBI	OMBARY	6	ANNONACEAE	*ISOLONA SP*
ZUBENUBI	VALOAKOHO	6	EUPHORBIACEAE	*OMPHALEA OPPOSITIFOLIA*
ZUBENUBI	VOAPAKA BERAVINA	6	CLUSIACEAE	*RHEEDIA SPP*
ZUBENUBI	ANTAFONANA	5	LAURACEAE	*OCOTEA SP*
ZUBENUBI	HAZONDOMOINE	5	EUPHORBICAEAE	*TANNODIA SP*
ZUBENUBI	LONGOTRA	5	LAURACEAE	*ASPIDOSTEMON SPP*
ZUBENUBI	MOLANGA	5	MALVACEAE	*DOMBEYA SP*
ZUBENUBI	MAIMBOLOHA	5	PITTOSPORACEAE	*PITTOSPORUM SP*
ZUBENUBI	TSIPATIKA	5	MORACEAE	*STREBULUS SPP*
ZUBENUBI	APANGA TREE	4	?	*PALM*
ZUBENUBI	AZININA	4	CLUSIACEAE	*SYMPHONIA SP*

Temperature and Humidity in Patch Zubenubi: The temperature was consistent from June to November averaging around 70°F although it was slightly hotter in November averaging around 79°F (Table 3.47). The lowest temperatures occurred in August (63°F). The humidity in June and August hovered around 75% while in the other months the humidity was 90% or above.

Table 3.47 Averages of daily temperature and humidity fluctuations in Patch Zubenubi

	8:00 AM	12:00 PM	3:00 PM
HUMIDITY AVERAGE	94.6%	86.8%	83.1%
TEMPERATURE AVERAGE	67.4°F	70.9°F	70.8°F

Zubenubi Patch Comparison

The predominant feature is the high density of lianas. The lianas in this patch form tangles at all levels and angles creating essentially one closed prominent canopy layer starting from the ground and extending up to 6.3 – 7.5 meters masking much of the vertical space. On average, 110 lianas were counted per 100 m^2 although in some areas the number of lianas is as high as 158/100 m^2. Patch Zubenubi has one of the lowest densities of 1-5 cm dbh trees (the other patch being the guava if focus on non-guava plants) (Table 3.48). Perhaps this is the case because of the over-abundance of lianas, which have a similar dbh and are filling this space. The density of 6 -10 cm dbh trees is moderate-to-high and the 11 to 20 cm and 21+ cm dbh tree densities are low (Table 3.48).

The 6 to 10 cm dbh trees are equally distributed from 1 to 3 meters apart. This distance is greater in comparison to other patches where the 6-10 cm dbh trees tend to be ≤1 meter apart. The 11-20 cm dbh trees are equally distributed or highly clumped at 1 to 2 meters. This pattern is also different from the other patches where these dbh trees tend to be equally distributed but at varying distances (Table 3.50). The 21+ cm dbh trees are equally distributed approximately 4 meters apart.

Table 3.48 Average number of varying dbh trees within 100 m^2 in the Zubenubi patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
12.8 (RANGE 9 – 16)	13.8 (RANGE 7 – 26)	5.3 (RANGE 3 – 7)	1.8 (RANGE 1 – 4)

The height of the first canopy layer is the tallest of all the patches. The height of the second canopy layer is also among the tallest heights (Table 3.49). The height of the third canopy level is moderate. Only the first canopy layer is connected. The second canopy layer has small gaps and the third layer has medium gaps in the canopy. Patch Zubenubi is the only patch to have consistent small gaps in the second canopy layer. There are several emergent trees on the periphery that reach some of the tallest heights among the patches quantified (the other patch being Fara).

Table 3.49 Canopy heights in Zubenubi patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	EMERGENT TREE HEIGHT
5.9 M (RANGE 5 – 6.3)	9.1 M (7.5 – 10.3)	12.3 M (11.3 – 13.1)	19.4 (17.5 – 20.3)

Table 3.50 Spatial distribution of trees of varying dbh

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL 1 TO 3 M	EQUAL/CLUMPED 1 TO 2 M	EQUAL 4 M

There is only one ravinala palm (11.9 meters in height). Other non-ravinala palms are also scarce (Table 3.51). Patch Zubenubi has the lowest density of herbaceous new growth and moderate densities of taller new growth treelets (Table 3.51). Zubenubi also exhibits one of the highest total counts of fallen and standing dead trees (N=21) (Table 3.8).

Table 3.51 Zubenubi patch characteristics presented as average number per 100 m^2

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25-1.9M	LIANAS	STANDING DEAD TREES	FALLEN DEAD TREES	PALMS
0.3 (RANGE 0 – 1)	70°F 79 °F	2.5 (RANGE 0 – 9)	1.3 (RANGE 0 – 5)	1 (RANGE 0 – 3)	110 (RANGE 84 - 158)	0.8 (RANGE 0 – 1)	4.5 (RANGE 3 – 5)	0.8 (RANGE 0 – 2)

PATCH SAHAKOHO: Sahakoho is located in the northwestern portion of the reserve. The sounds of an abutting village can be heard including people yelling, the chopping of firewood and roosters crowing. The canopy cover averages at 86.5% with three main levels. The first layer is connected at 5.4 meters. The second (11.9 meters) and third (16.4 meters) are both connected with some small gaps in the canopies. There are occasional emergent trees here at heights of 20.3 meters (0.25/100 m^2).

One-5 cm dbh (28.8/100 m^2) and 6-10 cm dbh (19.3/100 m^2) trees are prominent in this area with lianas being rare (6/100 m^2). The total count of lianas (N=24) is the lowest among the

patches (Table 3.58). These smaller dbh trees are less than 1 meter apart and they are equally distributed. Eleven-20 cm dbh (14.3/100 m^2) and 21+ cm dbh trees (6.8/100 m^2) are also equally distributed from 1 to 2 meters apart (Table 3.56). Ravinala palms are prominent (4 or 5/100 m^2) in this area with an average height of 11.3 meters. Apanga palms are also common in this area (9/100 m^2). Guava has spread to this area and five guava plants are growing in one of the plots and two in another plot. The most common plant is lalotina (Table 3.52).

The area to the west of this patch has increased amounts of guava, tree falls, and ravinala palms. The lower 1.9 to 3.8 meter layer is connected, forming vegetation tunnels in some sections. Dead fallen ravinala palm fronds also contribute to the full understory. There is a taller 9.4 meter layer with small gaps in the canopy in this adjacent area. This more degraded forest type continues until the edge of the reserve several kilometers to the west. *Eulemur* groups have been observed using this area.

An adjacent plot was quantified to the east of the Sahakoho patch for substrate comparison. The structure of this adjacent area may influence lemur variation of habitat use. This area is much denser with connected 3.8 meter, 6.3 meter, and 10.3 meter layers. There is also a 12.0 meter layer with medium gaps. More lianas are found here (38/100 m^2) that congregate on the ground and then extend up to and around trees at 6.3 meters forming a significant 5 to 6 cm dbh structural component. One-5 cm dbh (20/100 m^2), 6-10cm dbh (19/100 m^2), and 11-20 cm dbh (5/100 m^2) trees are all equally spaced ≤1 meter from one another. There are two dead trees and two fallen trees further contributing to the congested understory. The 21+ cm dbh trees (4/100 m^2) are equally spaced but further apart at 6 to 7 meters. Indri and sifaka groups move through here as they continue on to the north and south.

This adjacent area is also next to a 100 m^2 square of longoza. There is not much variety in plant species composition in this plot with the predominate tree being lalotina. There are also several afomena, guava, and ravinala trees in this patch taking advantage of the light gaps.

Trees of Economic and Ecological Value of Patch Sahakoho

One azinina (*Symphonia* sp.), one hazomainty (*Diospyros* sp.), four pallisandre (*Dalberigia* sp.), twelve ravinala (*Ravenala* sp.), seven guava (*Psidium* sp.), and three ramy trees were counted in this patch. The brown lemurs were observed to use the ramy trees as sleeping areas in the patch while the sifaka used the pallisandra trees as sleeping sites on occasion. The sifaka also were observed to eat mampay leaves, whereas *Eulemur* was not observed to engage any type of feeding behavior. The area adjacent to Patch Sahakoho also has trees of economic value including two azinina (*Symphonia* sp.), one fanzana (*Cyathea* sp.), four hasina (*Dracaena* sp.), six mampay (*Cynometra* sp.), twenty five hazomainty (*Diospyros* sp.), one ravinala (*Ravenala* sp.), and three voasirindrina (*Sorendea* sp.) trees

Table 3.52 Common trees found in patch Sahakoho

MALAGASY NAME	NUMBER	FAMILY	SPECIES
AFOMENA	3	MALVACEAE	*DOMBEYA SP*
AFOPOTSY	2	MALVACEAE	*GREWIA SP*
AMBONAMBONA	3	ARALIACEAE	*POLYSCIAS SP*
ANTAFONANA	4	LAURACEAE	*OCOTEA SP*
GUAVA	7	MYRTACEAE	*PSIDIUM CATTLEIANUM*
LALOTINA	104	EUPHORBIACEAE	*ANTHOSTEMA MADAGASCARIENSIS*
MAROANDRO	2	EUPHORBIACEAE	*BLOTIA SP*
PALLISANDRE	4	FABACEAE	*DALBERGIA GRAVEANA*
RAMY	3	BURSERACEAE	*CANARIUM MADAGASCARIENSIS*
RARA	8	MYRISTICACEAE	*BRONCHONEURA SP*
RAVINALA	12	STRELITZIACEAE	*RAVENALA MADAGASCARIENSIS*
SADOKA KELIRAVINA	3	RUBIACEAE	*GAERTNERA SP*
SOMOTRONANA	3	SAPINDACEAE	*STADMANIA SP*
TROVA	4	MORACEAE	*TRECULIA SP*
VOANTSILANA	2	ARALIACEAE	*POLYSCIAS SP*

Temperature and Humidity in Patch Sahakoho: Humidity was fairly consistent from June to November ranging from 83.0 to 95.0%. Temperature ranged from a low of 64° to a high of 76°F (Table 3.53). Temperature highs were in June (73°F) and November (76°F) and lows were in

August (64.6°F) and September (63.9°F). Patch Sahakoho has one of the highest temperature averages overall (the other being patch guava).

Table 3.53 Averages of daily temperature and humidity fluctuations in Patch Zubenubi

	8:00AM	12:00PM	3:00PM
HUMIDITY AVERAGE	94.4%	86.2%	87.6%
TEMPERATURE AVERAGE	68.5°F	70.5°F	70.6°F

Sahakoho Patch Comparison

The density of 1-5 cm dbh trees in Patch Sahakoho is moderate-to-high in comparison to the other patches (Table 3.54). The densities of 6-10 cm, 11-20 cm, and 21+ cm dbh trees are the highest in this patch compared to the other patches quantified in this research (Table 3.54). The 6-10 cm and 11 – 20 cm dbh trees are equally spaced at less than 1 meter apart while the 21+ cm dbh trees are equally spaced at 1 to 2 meters apart (Table 3.56). Guava plants are starting to spread further north into this patch with a total of seven new trees in the quantified area of Patch Sahakoho.

Table 3.54 Average number of varying dbh trees within 100 m^2 in the Sahakoho patch

1 TO 5 CM DBH	6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
28.8 (RANGE 23 - 33)	19.3 (RANGE 12 – 23)	14.3 (RANGE 9 – 18)	6.8 (RANGE 4 – 10)

The canopy height of layer one is one of the tallest (the other patch being Zubenubi (Table 3.55) and the canopy heights of layers two and three are the tallest in comparison to the other patches. There is only one emergent tree (Table 3.55). The height of canopy layer one is connected while canopy layers two and three are connected with some small gaps.

Table 3.55 Average canopy heights in Sahakoho patch

CANOPY HEIGHT LAYER 1	CANOPY HEIGHT LAYER 2	CANOPY HEIGHT LAYER 3	EMERGENT TREE HEIGHT
5.4 M (RANGE 3.5 – 6.7)	11.8 M (RANGE 8.4 – 15.3)	16.4 M	19.1 M

Table 3.56 Spatial distribution of trees of varying dbh

6 TO 10 CM DBH	11 TO 20 CM DBH	21+ CM DBH
EQUAL <1 METER	EQUAL 1 METER	EQUAL 1 TO 2 METERS

The density of ravinala palms is higher here along with other palm species, especially apanga palms (Table 3.57). The liana density is the lowest (N=24). There are no standing dead trees and fallen dead trees are rare (N=1) (Table 3.57). The new tree growth is also moderate relative to other patches.

Table 3.57 Sahakoho patch characteristics presented as average number per 100 m^2

RAVINALA	TEMP LOW - HIGH	HERBS	NEW GROWTH ≤ 0.3M	NEW GROWTH 1.25-1.9M	LIANAS	STANDING DEAD TREES	FALLEN DEAD TREES	PALMS
3 (RANGE 1 – 5)	64°F 73°F	4.4 (RANGE 4.8 – 6.8)	1.2 (RANGE 0 – 4)	0.4 (RANGE 0 -1)	6 (RANGE 4 – 8)	0	0.25 (RANGE 0 – 1)	6.3 (RANGE 3 – 9)

Chapter Summary

The results indicate that there are quantifiable differences between the patches within BNR. The environmental heterogeneity that results from the changing properties of the landscape is an important factor in controlling biodiversity (Huston, 1994; 1999) that may contribute to the varying responses (positive or negative) of a species to habitat change. For example, many species require more than one type of habitat for different life stages or events and would consequently benefit from a heterogeneous landscape (Law and Dickman, 1998). Therefore, quantifying habitat attributes and the landscape pattern of a forest fragment is an essential step in understanding a particular species', community's, groups', or individuals' response to micro – and macrohabitat features that contribute to patch and landscape complexity.

These patches demonstrate differences in microhabitat as well as macrohabitat of the internal patch and surrounding area. For example, the guava patch has the highest abundance of

guava and one of the shorter canopy heights. It also has the widest gaps in the canopy among the taller canopy. Due to the lack of and or erratic nature of the canopy cover here the temperature was one of the hottest in comparison to the other patches. There are very few non-guava trees in this patch with the majority of the available substrates consisting of 5-7cm dbh oblique and horizontal clustered branches that overwhelm the vertical space. The other common tree in this patch is the ravinala palm. As such, tree composition diversity is low in the guava. This patch is also in close proximity to the local village, Rendrirendry.

Patch 800-900 is the most variable patch in terms of vegetative substrates. It is in a transition zone between the guava/degraded forest and areas of primary forest. Canopy height is still relatively low but has increased from the guava patch. There is also a relatively high number of patchily distributed ravinala palms and some persistent guava trees. This patch also consists of frequent (25%/100 m^2) pockets of viney bamboo often growing around the abundant dead fallen and dead standing trees.

Patch 1600 has the highest abundance of 1-5 cm dbh (non-guava trees) equally spaced trees and the lowest abundance of 6-10cm dbh trees. Ravinalas are rare and there is no guava or bamboo growth. It has some of the tallest canopy heights for all three layers. Liana growth is also abundant.

Patch Sahabefoza is the only patch with extensive longoza fields in close proximity. In addition, guava grows in pockets throughout the patch. It also has the closest proximity to a small river that runs 20 meters north of the patch boundary. The slope of the landscape is also variable ranging from 5 degrees in the valley to a 36 degree incline in some parts. One of the higher abundances of 6-10 cm dbh trees occurs here while the other tree diameter categories are lower in comparison to other patches. The first canopy layer is among the shortest, as well as the second and third layers. There are also abundant palm species (ravinala and pandanus) growing here.

Patch Fara has a sparse understory allowing for more vertical space at lower levels. It is the only patch to have four consistent canopy layers and the only patch to have small

gaps/connectedness in canopy layer one while layers two and three are both connected. The third canopy height is relatively taller and the tallest emergent trees grow in this patch. Fara has one of the highest densities of 11-20 cm dbh trees. Fara also has the highest density of herbaceous new growth and there are no standing dead or fallen dead trees in this patch.

Patch Betakonona often has a blanket of low cloud cover and is quite windy. The terrain in this part of the reserve is extremely undulant and steep. It also has one of the highest densities of 1-5 cm dbh trees (the other being Patch 1600). The canopy height for layer three is the tallest height at this level and there are no emergent trees in this patch. Canopy heights one and two are connected while the third canopy layer has small to medium gaps. Betakonona is the only patch where this canopy connectedness pattern is observed. There are no ravinalas, but there is a relatively high abundance of other palm taxa.

Patch Zubenubi has the highest abundance of lianas. The heights of the first and second canopy layers are the tallest among the patches. Zubenubi is the only patch to have consistent small gaps in the second canopy layer. There are also occasional emergent trees that reach some of the tallest heights (the other patch being Fara). This patch has the lowest abundance of herbaceous new growth and the highest abundance of dead standing and dead fallen trees.

Patch Sahakoho is located in the northwestern portion of the reserve in close proximity to the forest edge. Sounds of an abutting village can be heard from this patch. Sahakoho and the guava, are the only two patches where one can hear human activities. This patch has the highest abundance of 6-10 cm dbh, 11-20 cm dbh, and 21+ cm dbh trees that are in close proximity and equally spaced. Guava has spread into this area though it is not nearly as dense as what is found in the southern portion of BNR. The canopy heights of layer one (the other patch being Zubenubi) layer two, and layer three are among the tallest. There are no standing dead trees and fallen dead trees and herbaceous new growth are sparse. The area to the west of this patch (closer to the forest

edge) has increased amount of guava, tree falls, and ravinala palms. To the east, there are pockets of longoza.

The results also indicate that many of the plots include a variable number of trees of economic value. In some patches these same trees are also ecologically important to the lemurs. At the same time, some ecologically critical trees that may not necessarily be of value to humans may still be at risk given the proximity to trees of economic value. These factors may influence the degree of risk for ecosystem collapse in the different patches. A patch with a high abundance of trees with economic importance that are also vital to lemur survival may have a higher risk factor in contrast to a patch with few trees of economic value, which the lemurs do not rely upon for different activities. The human use of the tree could also influence this risk factor. Is the whole tree harvested for the hardwood or just the fruits or flowers? For example, the guava patch has abundant guava and ravinala trees in addition to two hazomafana trees. The brown lemurs frequently utilize all three of these trees, creating a high-risk scenario if these trees are removed. Furthermore, guava eradication programs have been discussed in order to remove this invasive species from BNR to halt its continued spread deeper into the forest. The pending removal of the guava from Patch Guava would essentially also remove this patch, placing the brown lemurs in an even higher risk situation. In the future, research initiatives will focus on the importance of each of these trees of economic value to local communities to more accurately assess the risk factor for each patch.

As previously discussed, an important area of current landscape ecology research is aimed at disentangling the effects of landscape composition (what and how much is there) and landscape configurations (how is it spatially arranged) on populations (Fahrig 1997; McGarigal and Cushman, 2002). Although creating a model is certainly important to help make sense of forest complexity and pattern and for a working component within which to implement conservation management, it is important to also realize these models need constant new data sets and need to have the ability

to change and adapt to complex ecosystems. This is the value of GIS modeling in understanding or even making predictions based on current knowledge of a pending ecosystems' collapse or how the landscape changes through time in order to modify planning to the current situation or threat. GIS also allows for the analysis of multiple levels of threat (e.g. health, proximity to villages, trees of economic and ecological value). A GIS map illustrating the quantified patches of BNR is presented below (Figure 3.4).

A detailed assessment of the structural variation within BNR provides a framework within which to assess variation in lemur community structure, the focus of the next chapter.

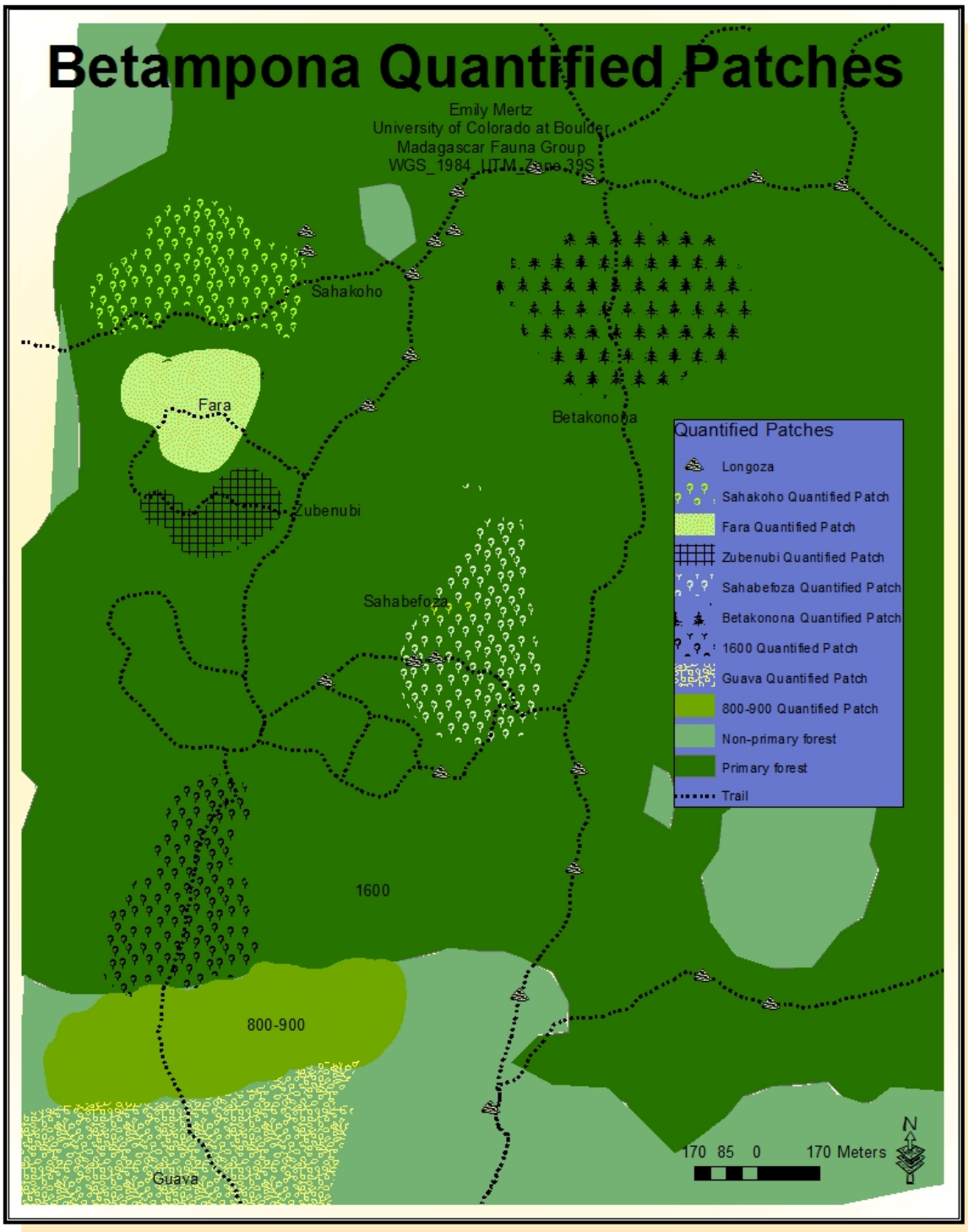


Figure 3.4 GIS map of quantified patches in BNR

CHAPTER 4
ANALYSIS OF LEMUR COMMUNITY STRUCTURE FROM POINT COUNTS WITHIN QUANTIFIED PATCHES

Overview of Chapter

The previous chapter demonstrated that the landscape of BNR is heterogeneous from the perspective of eight quantified patches. This chapter discusses the differences in lemur community structure (species richness, composition, and abundance) observed using all-day fixed radius (50 m) point counts within these eight quantified patches. By quantifying the patches I was able to define and control the structural variables and vegetation type that characterize each patch. This methodology was essential to determine if variation exists among lemur taxa patch utilization within the landscape of BNR. Moreover, by conducting point counts within each patch I was able to assess use by the entire community of five diurnal lemur taxa found within BNR. This chapter presents the lemurs that were observed in each of the quantified patches and addresses the variation in composition, richness, and abundance.

Other animals incidentally observed in the patches during point counts were documented. This information is presented below. Birds are abundant in BNR and are found throughout the different patches. Bird identifications are not my specialty so it is likely that habitat use by the many bird species that occupy BNR is severely underestimated in the point count surveys. Only the well-known species that I could identify are represented. To fully appreciate the variation of bird taxa utilizing the different patches, a separate research project should be devoted to their importance. Animals captured via camera traps in each of the patches are also noted.

Simpson's index (D) (Simpson, 1949) (Figure 4.1) was used to quantify the lemur diversity in each patch (Table 4.1). Simpson's Index is a measure that accounts for both richness and evenness. Richness is the number of different types of organisms in a given area. Species evenness refers to how close in number each organism in an area is to one another. For example, two samples may have the same richness number. However, in one of the samples one type of organism

may account for a larger proportion of the entire sample size. The latter sample would be considered less diverse because the organisms are not equitable. Communities of organisms that are dominated by one or two species are considered less diverse than communities that demonstrate similar abundances of several different organisms. Table 4.1 lists the Simpson's index (D), along with abundance, richness (S), and evenness (E) of lemur diversity in each quantified patch. A discussion of species diversity within each patch in the following paragraphs will refer back to the indices indicated in Table 4.1.

Simpson's Index = $\Sigma \left(\frac{ni}{NT}\right)^2$

n = the total number of organisms of a particular taxon in an area

N= the total number of organisms of all taxa in an area

0 = infinite diversity

1 = no diversity

Figure 4.1 Simpson's Index

Table 4.1 Lemur taxa abundance, richness, and evenness in different patches in BNR

Patch Name	Total Abundance	Richness (S)	Evenness (E)	Simpson's Index (D)
Guava	87	1	1	1
1600	56	2	0.43	0.87
Sahabefoza	41	2	0.41	0.82
Zubenubi	52	2	0.37	0.74
Sahakoho	22	3	0.17	0.52
800-900	50	3	0.16	0.47
Fara	55	4	0.11	0.42
Betakonona	28	3	0.13	0.39

Animals Observed from Point Counts in the Guava Patch

A number of different nocturnal and diurnal animals utilized the guava (Table 4.2). Vasa parrots (*Coracopsis* sp.) were commonly found in the guava, especially when ravinala seeds and flowers were available for consumption. Many other bird species, including owls, were found in the guava. The owls were potentially benefiting from the abundant insects and mouse lemurs. Several

species of chameleon were observed moving through the leaf litter, including *Brookesia supersilliarus* and *B. minimas*. A variety of skinks were also found here basking in the ample sunlight that filters through the canopy gaps and reaches the forest floor.

The only lemur observed to use the guava during the point counts was *Eulemur fulvus albifrons*. *Eulemur* used the guava and associated ravinala trees to move, sleep, and forage for food. A group of eight individuals, in particular, used the guava and the fruit trees in and around Rendrirendry on a regular basis. A total of 87 brown lemur observations were made.

Outside of the point count session, a group of three *Hapalemur griseus* were observed to use large bamboo clusters growing on the edge of the forest. These bamboo thickets also extend into the village Rendrirendry. The bamboo lemurs were never observed to use the guava itself. Opportunistic observations of *Microcebus rufus* were made at night in the guava. The mouse lemurs were observed to use the thick guava and liana tangles as an arboreal highway. *Lepilemur mustelinus* was also observed to use the peripheral trees of the guava close to the village edge.

No lemurs were recorded via the camera traps, although several diurnal birds and nocturnal forest rats were captured as they passed through the patch.

Table 4.2 Animals observed in the guava from point counts

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/14/09	*CORACOPSIS*	0	>20	?
6/14/09	*EULEMUR*	0	5	2 FEMALE 3 MALE
6/14/09	*EULEMUR*	0	5	2 FEMALE 3 MALE
6/14/09	*EULEMUR*	0	5	1 MALE 4 FEMALE
6/14/09	*EULEMUR*	0	5	1 MALE 4 FEMALE
6/23/09	*EULEMUR*	0	8	4 MALE 4 FEMALE
6/23/09	*CORACOPSIS*	0	>20	?
6/24/09	*EULEMUR*	0	5	3 MALE 2 FEMALE
6/24/09	*EULEMUR*	0	6	?
6/24/09	*EULEMUR*	0	4	2 MALE 2 FEMALE
6/24/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
6/24/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
6/24/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
6/24/09	*EULEMUR*	0	8	2 FEMALE 4 MALE
6/24/09	*BROOKESIA*	0	1	MALE
6/24/09	*EULEMUR*	0	2	2 MALE

6/24/09	*EULEMUR*	0	2	2 FEMALE
6/24/09	*CORACOPSIS*	0	>20	?
7/29/09	*EULEMUR*	0	8	4 MALE 4 FEMALE
7/29/09	*EULEMUR*	0	>20	?
8/18/09	*EULEMUR*	0	2	2 MALE
8/18/09	*CORACOPSIS*	0	>20	?
8/18/09	*BROOKESIA*	0	1	MALE
9/5/09	*EULEMUR*	0	5	2 FEMALE 3 MALE
9/5/09	*CORACOPSIS*	0	>20	?
10/10/09	*EULEMUR*	0	1	1 MALE
10/10/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
10/10/09	*CORACOPSIS*	0	>20	?
10/21/09	*EULEMUR*	0	2	2 FEMALE
10/21/09	*EULEMUR*	0	4	2 MALE 2 FEMALE
10/21/09	*CORACOPSIS*	0	>20	?
11/17/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
11/17/09	*CORACOPSIS*	0	>20	?

Lemur Species Richness, Composition, and Abundance in the Guava

The guava patch had the highest density of lemurs, although this density was composed of one taxon, *Eulemur*. As a result, lemur species diversity was very low in the guava (D = 1, E = 1) (Tables 4.1, 4.3). *Eulemur* was quite abundant in the guava and was commonly seen moving, eating, and resting there. Although *Eulemur* was the only lemur observed inside of the guava patch during the point counts, other lemur taxa were observed opportunistically to use the periphery region of the reserve as well as areas inside of the village Rendrirendry. Because of this, species diversity could increase if the guava patch and peripheral area were quantified collectively as a spatial area of utilization. For example, *Hapalemur* was never observed in the guava patch itself during a point count session. Rather, *Hapalemur* was observed outside of the guava on the periphery of the reserve and in the village Rendrirendry. *Hapalemur* primarily ate the bamboo that grew in thick bushes in the northern section of the village. *Lepilemur* was also observed using the trees peripherial to the guava patch and close to the village. *Lepilemur* individuals often froze when sighted. Behaviors conducted along the guava perimeter by the sportive lemurs remain unknown. *Lepilemur* vocalizations were heard at night in the village from those individuals utilizing the surrounding areas. For consistency, the diversity indices in the guava were based on observations

made of diurnal lemurs observed during a point count session.

Table 4.3 Summary of lemur composition and abundance found in guava patch during point counts.

LEMUR TAXA	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
EULEMUR	87	Group of 2, 5, 8

Animals Observed from Point Counts in Patch 800-900

A variety of animals were observed utilizing this patch area, including goshawks (*Accipiter* sp.), vasa parrots, brown mongoose (*Salanoia* sp.), and lemurs (Table 4.4). *Eulemur* and *Hapalemur* were the most common diurnal lemur taxa (Table 4.5). A group of two *Propithecus* was seen twice moving through this part of the forest (in plot 3, which is the transition area to more primary forest), marking trees as they moved from the southeast near plot 4 up through plot 1 heading in a northeastern direction. On both occasions the sifaka traveled in this transition area between more degraded forest and the border of primary forest. Sifaka were never observed to occupy the space south of this transitional area. No animals were captured via camera traps in this patch.

Table 4.4 Animals observed in patch 800-900

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/17/09	*ACCIPITER*	0	1	?
6/17/09	*CORACOPSIS*	0	>10	?
6/17/09	*EULEMUR*	0	3	?
6/17/09	*PROPITHECUS*	0	2	1 FEMALE 1 MALE
6/17/09	*EULEMUR*	0	2	3 FEMALE 2 MALE
6/17/09	*EULEMUR*	0	5	3 FEMALE 2 MALE
6/17/09	*EULEMUR*	0	3	1 FEMALE 2 MALE
6/27/09	*EULEMUR*	0	4	1 FEMALE 3 MALE
6/27/09	*CORACOPSIS*	0	>10	?
6/27/09	*SALANOIA*	0	1	?
7/6/09	*EULEMUR*	0	4	2 FEMALE 2 MALE
8/15/09	*PROPITHECUS*	0	2	?
8/15/09	*EULEMUR*	0	4	2 FEMALE 2 MALE

8/29/09	*EULEMUR*	0	2	2 MALE
10/10/09	*HAPALEMUR*	0	4	?
10/21/09	*EULEMUR*	0	1	1 MALE
10/21/09	*HAPALEMUR*	0	4	?
11/17/09	*HAPALEMUR*	0	4	?
11/17/09	*EULEMUR*	0	2	1 FEMALE 1 MALE

Lemur Species Richness, Composition, and Abundance in Patch 800-900

Patch 800-900 had an overall moderate total abundance of lemurs (Table 4.5). Three lemur taxa were observed using this area giving a Simpson's index of 0.47, indicating moderate diversity. The lemur taxa were not equitably distributed in this patch (E = 0.16), decreasing the diversity in this patch even further. *Eulemur* and *Hapalemur* were the most common diurnal lemur taxa (Table 4.5) with *Eulemur* the most abundant. A group of two sifaka was also seen twice moving through this part of the forest.

Table 4.5 Summary of lemur composition and abundance found in 800-900 patch during point counts

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
EULEMUR	30	2, 4, 5
PROPITHECUS	4	2
HAPALEMUR	16	4

Animals Observed from Point Counts in Patch 1600

Eulemur groups were predominant in this patch. *Propithecus* was also observed eating flowers on one occasion as well as moving through this patch. Blue coua (*Coua* sp.), fossa (*Cryptoprocta* sp.), forest rats (*Nesomys* sp.), a bush pig (*Potamochoerus* sp.), and brown-tailed mongoose were also observed in this area (Table 4.6). No animals were captured via camera traps in this patch.

Table 4.6 Animals observed in patch 1600

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/12/09	*NESOMYS*	0	2	?
6/12/09	*EULEMUR*	0	5	3 MALE 2 FEMALE
6/12/09	*EULEMUR*	0	5	3 MALE 2 FEMALE
6/12/09	*COUA*	0	4	?
6/22/09	*EULEMUR*	0	5	3 MALE 2 FEMALE
7/3/09	*CRYPTOPROCTA*	0	2	?
7/4/09	*COUA*	0	2	?
7/4/09	*EULEMUR*	0	8	4 MALE 4 FEMALE
8/17/09	*EULEMUR*	0	4	1 MALE 3 FEMALE
8/17/09	*NESOMYS*	0	1	?
8/17/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
8/25/09	*PROPITHECUS*	0	3	2 FEMALE 1 MALE
9/1/09	*EULEMUR*	0	5	3 MALE 2 FEMALE
10/9/09	*EULEMUR*	0	4	2 MALE 2 FEMALE
10/12/09	*SALANOINA*	0	2	?
10/12/09	NO LEMURS	0	0	?
10/12/09	*POTAMOCHOERUS*	0	1	?
10/20/09	*PROPITHECUS*	0	1	1 MALE
11/23/09	*EULEMUR*	0	7	3 MALE 4 FEMALE
9/1/09	*EULEMUR*	0	7	3 MALE 4 FEMALE

Lemur Species Richness, Composition, and Abundance in Patch 1600

The total lemur abundance was high in patch 1600 (Tables 4.1, 4.7). This abundance number is largely represented by one taxon, *Eulemur*. Therefore, lemur species diversity is low (D = 0.87) in patch 1600, unevenly represented by two taxa (E = 0.43) (Table 4.7).

Table 4.7 Summary of lemur composition and abundance found in 1600 patch during point counts

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
EULEMUR	52	4, 5, 7
PROPITHECUS	**4**	**1, 3**

Animals Observed from Point Counts in Patch Sahabefoza

A variety of animals were observed to use this patch (Table 4.8). *Eulemur* groups were the most common lemur taxa (Table 4.9), primarily eating fruit and resting in two famelona (*Chrysophyllum* sp.) trees adjacent to the longoza field. When there was no longer fruit available for

consumption, the brown lemurs still rested in and used these trees to move. Closer to the river, in the valley area of this patch, the brown lemurs frequently rested in a molanga (*Dombya* sp.) tree.

When the brown lemurs moved, the lemurs often headed to the west using the smaller trees and low lying liana tangles lining the longoza field. Alternatively, the lemurs moved north towards the valley and then headed east before reaching the river. At this point they moved again through the low lying trees/shrubs and liana tangles adjacent to a smaller patch of longoza.

Several groups of *Hapalemur* were also observed moving through this patch. *Hapalemur* in contrast to *Eulemur*, moved right through the longoza field at about half a meter from the ground, vertical-clinging-and-leaping from one support to the next.

Three *Varecia* were observed and also heard giving their roar/shriek chorus from several 25 meter partially dead trees that were abutting the longoza field to the west. After the vocalization stopped, the group continued off to the west. *Varecia* was never observed moving through or using this patch. Different *Indri* groups were also heard calling to the south and north, but individuals were never observed in the patch. Two of the radio-collared *Indri* groups' ranges were close to the eastern perimeter of this patch and to the south past the longoza field.

Several brown-tailed mongooses were observed looking through the leaf litter closer to the valley and smaller patch of longoza. Several bush pigs were observed running out of the longoza. Bush pigs also turn up the mud and create tunnels of broken longoza stems, which were indirect indicators of their use of this area. The camera traps posted in this patch took a single picture of a bamboo lemur moving through the valley portion of this patch.

Table 4.8 Animals observed in patch Sahabefoza

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/13/09	*SALANOIA*	0	1	?
6/13/09	NO LEMURS[7]	0	0	0
6/23/09	*EULEMUR*	0	6	?
6/23/09	*EULEMUR*	0	4	?
7/11/09	*EULEMUR*	0	7	?
8/8/09	*EULEMUR*	0	4	2 FEMALE 1 MALE
8/8/09	*EULEMUR*	0	2	1 FEMALE 1 MALE
8/8/09	*INDRI*	SOUTH	1	1 FEMALE
8/8/09	*HAPALEMUR*	0	4	?
9/4/09	*EULEMUR*	0	3	1 FEMALE 2 MALE
9/26/09	NO LEMURS	0	0	0
10/26/09	*INDRI*	NORTH	?	?
10/26/09	*SALANOIA*	0	2	?
10/26/09	*EULEMUR*	0	2	1 FEMALE 1 MALE
10/26/09	*VARECIA*	WEST	2	?
10/26/09	*POTAMOCHOERUS*	0	1	?
10/26/09	*EULEMUR*	0	5	?
11/18/09	*EULEMUR*	0	4	2 FEMALE 2 MALE
11/18/09	*HAPALEMUR*	0	3	?

Lemur Richness, Composition, and Abundance in Patch Sahabefoza

Patch Sahabefoza had a moderate total abundance of lemurs (Tables 4.1, 4.9). But, similar to other patches, *Eulemur* was the taxon that dominated this abundance number (Table 4.9). The species diversity was low in this patch (D = 0.82) unequally represented by two lemur taxa (E = 0.41) (Tables 4.1, 4.9).

Table 4.9 Summary of lemur composition and abundance found in Sahabefoza patch during point counts

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
EULEMUR	37	2, 4
HAPALEMUR	4	4

[7] On occasion, no lemurs were observed during a point count session in a patch. Due to the primary focus on diurnal lemurs in this research, only the non-observation of lemurs is indicated in the tables.

Animals Observed from Point Counts in Patch Fara: A variety of animals were observed to use Patch Fara, including blue couas, brown-tailed mongoose, and four of the five diurnal lemur species (Table 4.10). *Varecia*, *Propithecus*, *Eulemur*, and *Hapalemur* were all observed in this patch (Table 4.11). *Indri* groups were never observed using the patch, but were heard calling to the southwest and to the north. *Varecia* groups were also heard calling to the northeast and the northwest. No animals were captured via camera traps in this patch.

Table 4.10 Animals observed in patch Fara

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/11/09	*COUA*	0	5	?
6/11/09	*SALANOIA*	0	2	?
6/11/09	*VARECIA*	0	3	?
6/11/09	*PROPITHECUS*	0	3	?
6/15/09	*HAPALEMUR*	0	2	?
6/21/09	*VARECIA*	0	4	?
6/21/09	*EULEMUR*	0	8	5MALE 3FEMALE
7/1/09	*EULEMUR*	0	8	5MALE 3FEMALE
7/1/09	*PROPITHECUS*	0	3	?
8/5/09	*EULEMUR*	0	4	?
8/5/09	*HAPALEMUR*	0	3	?
8/28/09	*EULEMUR*	0	1	MALE
9/29/09	*HAPALEMUR*	0	5	3 ADULT 2 BABY
9/29/09	*INDRI*	NORTH	?	?
9/29/09	*VARECIA*	NORTHEAST	?	?
11/12/09	*EULEMUR*	0	5	3 FEMALE 2 MALE
11/12/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
11/19/09	*HAPALEMUR*	0	5	?
11/19/09	*VARECIA*	NORTHWEST	?	?
11/19/09	*INDRI*	SOUTHWEST	?	?
11/19/09	*VARECIA*	0	1	?
11/19/09	*EULEMUR*	0	4	2 MALE 2 FEMALE

Lemur Species Richness, Composition, and Abundance in Patch Fara

Patch Fara was one of the most diverse (D = 0.42) (the other being Patch Betakonona) patches represented by four diurnal lemur taxa (Table 4.11). The total abundance of lemurs was also high in comparison to the other patches (Table 4.1). *Eulemur*, once again, was the most

abundant in this patch, followed by *Hapalemur* and then *Varecia* and *Propithecus* (E = 0.11) (Table 4.11).

Table 4.11 Summary of lemur composition and abundance found in Fara patch during point counts

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
EULEMUR	**32**	**4, 8**
HAPALEMUR	**15**	**5**
PROPITHECUS	**3**	**3**
VARECIA	**5**	**1, 4**

Animals Observed from Point Counts in Patch Betakonona: *Propithecus*, *Eulemur*, and *Indri* were observed using this patch. *Indri* groups were often heard calling back and forth to the west and east. *Varecia* groups were also heard calling to the east. One group of *Avahi* was observed feeding, moving, and resting in the mid-to-late afternoon, which was interesting given their primary nocturnal activity budget. Several brown-tailed mongoose individuals were seen using the forest floor as well as traveling along branches in the canopy at a height of 10 meters (Table 4.12). The camera traps posted in this patch took a series of photos of a single diademed sifaka moving past the camera. This was the only lemur (or animal) in this patch to be captured via camera trap.

Table 4.12 Animals observed in Patch Betakonona

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/18/09	*PROPITHECUS*	0	5	?
6/29/09	*INDRI*	WEST	2	?
6/29/09	*SALANOIA*	0	2	?
6/29/09	NO LEMURS	0	0	?
7/22/09	*PROPITHECUS*	0	1	?
7/22/09	*INDRI*	EAST	?	?
7/22/09	*EULEMUR*	0	4	2 FEMALE 2 MALE
8/21/09	*INDRI*	0	3	?
9/4/09	*EULEMUR*	0	2	1 FEMALE 1 MALE
9/4/09	*SALANOIA*	1	1	?
10/3/09	*EULEMUR*	0	7	2 FEMALE 5 MALE
10/3/09	*SIFAKA*	0	2	?
10/3/09	*INDRI*	0	3	?
10/27/09	*INDRI*	0	3	?
10/27/09	*PROPITHECUS*	0	3	?

11/13/09	*VARECIA*	EAST	?	?
11/13/09	*AVAHI*	0	3	?

Lemur Species Richness, Composition, and Abundance in Patch Betakonona

Patch Betakonona was one of the most species diverse (D = 0.39) (the other being Patch Fara) patches, represented by four different lemur taxa (Table 4.13). The total abundance of lemurs observed, however, was towards the lower end in a comparison with the other patches (Tables 4.1, 4.13). *Eulemur* and *Indri* were the most abundant diurnal lemurs followed by *Propithecus* (E = 0.13). *Avahi* was not included in Simpson's index because of the overall focus on diurnal lemur taxa.

Table 4.13 Summary of lemur composition and abundance found in Patch Betakonona during point counts

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
EULEMUR	13	2, 4. 7
INDRI	11	3
PROPITHECUS	4	1, 3, 5
AVAHI	3	3

Animals Observed from Point Counts in Patch Zubenubi

There were a number of different bird taxa (e.g. *Cinnyris* sp.) that congregated and foraged in the space between Patch Zubenubi and the adjacent area in the mornings. After 10:00 AM this area became oddly quiet and still with very little animal activity or vocalizations. Blue couas (Table 4.14) frequented this area throughout the day, rifling through the leaf litter on the forest floor or foraging by hopping from branch to branch in the canopy. *Indri* and *Eulemur* were the only lemurs observed in the area. *Indri* groups were also heard calling from the west and north. Additionally, *Varecia* groups were heard calling from the north.

Table 4.14 Animals observed in Patch Zubenubi

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/16/09	*VARECIA*	NORTHWEST	?	?
6/16/09	*INDRI*	WEST	?	?
6/16/09	*INDRI*	WEST	?	?
6/16/09	*COUA*	0	2	?
6/16/09	*INDRI*	0	3	?
6/16/09	*COUA*	0	3	?
6/26/09	*VARECIA*	NORTHWEST	?	?
6/26/09	*COUA*	0	3	?
6/26/09	NO LEMURS	0	0	?
6/26/09	*COUA*	0	2	?
7/18/09	*COUA*	0	1	?
7/18/09	*EULEMUR*	0	2	1 MALE 1 FEMALE
7/18/09	*INDRI*	0	2	?
7/18/09	*COUA*	0	1	?
8/19/09	*EULEMUR*	0	4	3 FEMALE 1 MALE
9/19/09	*EULEMUR*	0	5	1 FEMALE 4 MALE
9/19/09	*VARECIA*	NORTH	?	?
10/1/09	*INDRI*	NORTH	?	?
10/1/09	*EULEMUR*	0	4	2 FEMALE 2 MALE
10/1/09	*COUA*	1	3	?
10/1/09	*EULEMUR*	0	6	3 FEMALE 3 MALE
11/12/09	*EULEMUR*	0	4	2 FEMALE 2 MALE
11/12/09	*INDRI*	0	3	?
11/12/09	*EULEMUR*	0	3	1 FEMALE 2 MALE
11/12/09	*COUA*	0	2	?
11/12/09	*EULEMUR*	0	4	1 FEMALE 3 MALE
11/19/09	*EULEMUR*	0	4	3 FEMALE 1 MALE
11/19/09	*EULEMUR*	0	3	1 FEMALE 2 MALE
11/19/09	*EULEMUR*	0	5	3 FEMALE 2 MALE
11/19/09	*COUA*	0	1	?

Lemur Species Richness, Composition, and Abundance in Patch Zubenubi

Patch Zubenubi's lemur species abundance was elevated, but species diversity was low (D = 0.74) (Table 4.1). Two lemur taxa were observed to use Patch Zubenubi, although *Eulemur* abundance was much greater than *Indri* abundance (E = 0.37). The *Eulemur* abundance drove the elevated abundance observed in Patch Zubenubi (Table 4.15).

Table 4.15 Summary of Lemur Composition and Abundance found in Patch Zubenubi

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
INDRI	**8**	**3**
EULEMUR	**44**	**3, 4, 5**

Animals Observed from Point Counts in Patch Sahakoho: Vasa parrots were prominent in this area and were often heard flying above on all point count sessions. The parrots predominately ate ravinala seeds or rested on ravinala palms while in this patch. Blue couas were also observed to use this area on all point count sessions picking through the leaf litter on the forest floor. *Propithecus*, *Eulemur*, and *Indri* used this patch. *Indri* groups were heard calling from the north and east. Additionally, *Varecia* groups were heard calling from the eastern, northeastern, and the southern portions of the reserve (Table 4.16). The camera traps posted in this patch took pictures of an *Avahi* on two separate occasions. One photo was of a single individual and the other photo was of an adult and infant. *Avahi* was the only lemur (or animal) captured by camera traps.

Table 4.16 Animals observed in Patch Sahakoho

DATE	ANIMAL SEEN	ANIMAL HEARD	NUMBER	MALE/FEMALE
6/15/09	*COUA*	0	4	?
6/15/09	*CORACOPSIS*	0	>10	?
6/25/09	*INDRI*	0	3	?
6/25/09	*CORACOPSIS*	0	>20	?
7/14/09	*CORACOPSIS*	0	>10	?
7/14/09	*COUA*	0	6	?
7/14/09	*INDRI*	NORTH	?	?
7/14/09	*VARECIA*	EAST	?	?
8/22/09	*PROPITHECUS*	0	1	FEMALE
8/22/09	*CORACOPSIS*	0	>20	?
9/2/09	*NO LEMURS*	0	0	0
9/2/09	*CORACOPSIS*	0	>20	?
9/25/09	*EULEMUR*	SOUTH	?	?
9/25/09	*VARECIA*	NORTHEAST	?	?
9/25/09	*INDRI*	NORTH	?	?
9/25/09	*INDRI*	EAST	?	?
9/25/09	*EULEMUR*	0	4	2 MALE 2 FEMALE
9/25/09	*CORACOPSIS*	0	>20	?
10/17/09	*PROPITHECUS*	0	3	2 FEMALE 1 MALE
10/17/09	*CORACOPSIS*	0	>10	?
10/17/09	*EULEMUR*	0	2	1 MALE 1 FEMALE

10/17/09	*EULEMUR*	0	3	1 MALE 2 FEMALE
10/17/09	*VARECIA*	SOUTH	?	?
10/17/09	*EULEMUR*	0	3	2 FEMALE/INFANT 1 MALE
11/16/09	*INDRI*	NORTH	?	?
11/16/09	*VARECIA*	SOUTH	?	?
11/16/09	*CORACOPSIS*	0	>20	?

Lemur Species Richness, Composition, and Abundance and Patch Sahakoho

Patch Sahakoho had the lowest total number of lemurs (Table 4.1), but relative to the other patches, Sahakoho had a moderately high species diversity (D = 0.52) (Tables 4.1, 4.16). *Eulemur* was the most abundant taxa here followed by *Indri* and *Propithecus* (E = 0.17) (Table 4.17).

Table 4.17 Summary of Lemur Composition and Abundance found in Patch Sahakoho

LEMUR	TOTAL NUMBER OF INDIVIDUALS OBSERVED	MOST COMMON GROUP SIZE
INDRI	**3**	**3**
EULEMUR	**15**	**2, 3, 4**
PROPITHECUS	**4**	**1, 3**

Chapter Summary

The goal of this chapter was to answer one question. Are there differences in lemur species community structure within the quantified patches? The results indicate that there is variation among diurnal lemur species richness, composition, and abundance throughout the different quantified patches. A summary of these results is presented below.

Eulemur: *Eulemur* utilized all of the quantified patches, although this utilization occurred at varying degrees. The highest abundances of brown lemurs occurred in Patch Guava and Patch 1600. The lowest abundances occurred in Patches Betakonona and Sahakoho.

Hapalemur: *Hapalemur* utilized three out of the eight patches (800-900, Sahabefoza, and Fara). Though, bamboo lemurs also used the periphery of the reserve and areas that abut the local village, Rendrirendry (discussed further in section about Patch Guava). *Hapalemur* had the highest abundances in patches 800-900 and Fara, with the lowest abundance occurring in Patch

Sahabefoza. A single individual was also photographed via the camera trap placed inside of Patch Sahabefoza.

Propithecus: *Propithecus* utilized five out of the eight patches (Betakonona, Sahakoho, 800-900, Fara, and 1600). The abundance of sifaka was consistently low in all of the patches lingering around only three or four individuals. A camera trap captured a single sifaka moving through Patch Betakonona.

Varecia: *Varecia* was observed to only utilize one patch (Patch Fara). Although *Varecia* was often heard some distance away, ruffed lemur individuals were rarely seen during point counts or even among opportunistic sightings while in the forest.

Indri: *Indri* utilized three out of the eight quantified patches (Betakonona, Zubenubi, and Sahakoho). The highest abundances of *Indri* occurred in patches Betakonona and Zubenubi, while the lowest abundance occurred in Patch Sahakoho.

Avahi: *Avahi* (a group of three) was observed to utilize only Patch Betakonona during the point count sessions. In addition, a single individual on one occasion and an individual carrying an infant on a different occasion were caught via the camera trap in Patch Sahakoho.

This chapter revealed that there are differences in diurnal lemur community structure within the quantified patches of BNR. The diversity index for each patch also varied. The most diversity was observed in patches Fara and Betakonona with the least diversity in the Guava. The species evenness (average proportion of the total of each species squared) generally followed Simpson's D for each patch with the more diverse patches also expressing more species evenness. The next chapter explores the role of microhabitat, macrohabitat, and landscape scale vegetation characteristics as a means to understand this variation.

CHAPTER 5
ANALYSIS OF BEHAVIORAL DATA FROM POINT COUNTS IN RELATION TO DIFFERENT SPATIAL SCALES

Overview of Chapter

The results of the previous chapter indicate that there is variation in lemur species composition and abundance among the quantified patches. Chapter 5 explores the role of microhabitat, macrohabitat, and landscape scale vegetation characteristics in this variation. This is accomplished by first presenting a detailed description of the behavioral data, substrate use, and activity budget recorded from each taxon of lemur that utilized the different quantified patches during the point count sessions. These descriptions are then followed by a comparative analysis of the different lemur taxa and what patches they were and were not using, including a discussion of the different substrates, heights, and quadrants used for their overall activities (i.e. resting, eating, moving). Instantaneous focal animal sampling at two minute intervals was used to collect behavioral data (as discussed in Chapter 2). A table defining the size range for the substrates and height categories, tree quadrants, and an ethogram can be found in the appendix. This provides insight into what the possible limiting factors are in each patch, which in turn may dictate the different lemur taxa using or not using a particular patch. The analysis of differential lemur patch use will focus on the following questions:

- What patches are the lemurs found in?
- Are there certain patches the lemurs utilize more than others?
- What are the lemurs doing in these patches?
- Are there intra-species differences in the behaviors observed of the lemurs within different patches? For example, in certain patches brown lemurs may focus more of their time on eating and less time on resting, whereas in other patches brown lemurs may spend more time moving and less time resting. Why is this? Is the microhabitat an important contributing factor to lemur patch use? Or, is the macrohabitat more influential?

BEHAVIORAL DATA FROM PATCHES

PATCH GUAVA
Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: Very small 66.1%, Small 25.7%, Medium 8.2%
Overall height of substrate: A 28.4%, B 44.3%, C 9.3%, D 14.8%, E 3.3%
Overall quadrant: Guava thickets 42%, Quad 3 12.6%, Quad 4 9.3%, Rav leaf 6 7.7%
Overall orientation: A 27.9%, B 62.3%, C 9.8%
Overall behaviors: Eat fruit 7.1%, Eat flowers 10.4%, Eat Leaves 0%, Move 32.2%, Rest 31.7%, Threat 16.4%
Total tree height: B 32.8%, C 38.8%, D 14.8%, E 12%, F 1.6%

The only lemur observed to use the guava were groups of *Eulemur*. The brown lemur groups varied in size from two to eight individuals as well as in composition. Overall, *Eulemur* spent 17.5% of their total activity budget eating food while in the guava patch. While eating, the substrate orientation used was horizontal (37%) or oblique (63%), and was small to medium in diameter. The foods *Eulemur* consumed here were flowers (51.4%), fruits (34.3%), and nectar (8.6%). *Eulemur* used a sit posture when eating ravinala flowers 54%[8] of the total amount of time at a height of two to three meters. The quadrant three was the primary location utilized while consuming the ravinala flowers. While eating fruit from other palm species, *Eulemur* stood (29%) on oblique (70%) and horizontal (30%) substrates at a height of six meters. The brown lemurs mainly used quadrant one for this position and correlated behavior. *Eulemur* also occasionally ate flower nectar in some of the taller (6 m) ravinala palms.

Eulemur spent an equal amount of time resting and moving while in the guava. Moving was primarily by quadrupedal locomotion (66%) and less so by leaping short distances (<1 m) (19%). When moving quadrupedally or leaping short distances the brown lemurs traveled at a height of one meter (72%) on oblique, very small (<1 cm dbh) substrates (90%). When moving, the brown lemurs proceeded primarily through the thickest parts of the guava. When moving on non-guava substrates, they preferred quadrant three.

[8] Percentages are based on the total amount of time the lemur engaged in the particular position or behavior under discussion.

When resting, the brown lemurs often sat in close contact with their tails wrapped around each other's bodies (67%). The lemurs engaged in this posture and behavior at a height of two to three meters in the guava thickets on horizontal branches (67%) or oblique branches. *Eulemur* individuals varied in the height used for sitting and resting, but 50% of the time the lemurs sat and rested at a height of four to five meters. Half of the time the lemurs used horizontal substrates and the other half they used oblique as resting substrates. The brown lemurs used the ravinalas' strong palms or quadrant six in non-ravinala trees for these activities.

Interestingly, *Eulemur* groups that utilized the guava never appeared to habituate to human presence despite the frequent interaction of the two primates. Or rather, the brown lemurs were just agitated by human presence. As such, when *Eulemur* groups noticed humans in the area (though sometimes this would take up to 45 minutes), individuals often threatened by vocalizing and wagging their tails back and forth followed by a mad dash into the thickest impenetrable sections of the guava.

PATCH 1600
Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: Very small 21.5%, Small 68%, Medium 10.5%
Overall height of substrate: B 10.5%, C 9.3%, E 17.4%, F 15.4%
Overall quadrant: Quad3 16%, Quad4 55%, Quad5 12.6%
Overall orientation: A 5.7%, B 90.3%, C 4%
Overall behaviors: Eat fruit 18%, Eat leaves 2.4%, Groom-self 16.2%, Move 21.1%, Rest 35.2%, Threat 3.2%
Total tree height: E, 48.6%, F, 27.9%

Eulemur and *Propithecus* were the only two lemurs observed to use this patch. *Eulemur* groups commonly ate fruit from two key Zanamena (*Dialium unifoliolatum*) trees. While in this patch, *Eulemur* ate fruit 88% of the time out of their total feeding time. The other 12% was spent eating leaves. While eating fruit, *Eulemur* individuals were most often sitting at a height of nine to ten meters on medium substrates followed by a height of six meters on very small substrates. *Eulemur* also used suspensory and standing postures on very small branches to eat fruit. Oblique

substrates were used for almost all of the feeding behavior (94%). Most of the feeding behavior occurred in quadrant five (40%) with quadrants one and four also occasionally used.

Eulemur individuals were observed to rest more (63%) than move (37%) in this patch. These lemurs also spent 16% of their time out of their total activity budget grooming themselves at a substrate height of six meters. This contrasts with the brown lemurs using the guava, which did not engage in any type of grooming behavior. The primary means of moving was quadrupedal locomotion (71%) with the occasional leap of less than one meter to one meter. Very small and small sized substrates were most commonly used. *Eulemur* used oblique branches for quadrupedal locomotion, and when leaping, individuals used all orientations although longer distance leaps of one or two meters were often made on vertical supports. The main quadrupedal movement was at a height between six and eight meters while leaping occurred in a wider range of heights between two and ten meters.

When resting, the brown lemurs often sat in close contact with their tails wrapped around each other's bodies (87.5%). This was only done on small oblique substrates (100%) at heights of three (28.6%), six (46.8%), and eight (24.8%) meters. The brown lemurs often rested in quadrant three (23%) or four (66.7%).

Summary of substrate use and total activity budget for *Propithecus*:
Overall size of substrate: Large, 100%
Overall height of substrate: 7 meters, 100%
Overall quadrant: Quad7, 100%
Overall orientation: Vertical, 100%
Overall behaviors: Eat flowers, 100%
Total tree height: 10 meters (100%)

Only one group of *Propithecus* on a single occasion was observed to use this patch and the group happened to be radio-collared sifaka group 10. All three sifaka were eating flowers of the hasina tree by vertically clinging to a large tree trunk and then eating the flowers of the adjacent small substrate sized tree that was too flimsy to support the sifakas' body weight. All three were feeding at a height of seven meters in a tree with a height of ten meters.

PATCH SAHABEFOZA
Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: A 7.8%, B 87.2%, C 5.0%
Overall height of substrate: B 1.7%, C 3.9%, D 29.1%, E 58.1%, F 7.3%
Overall quadrant: Quad1 40.8%, Quad3 12.3%, Quad4 19.6%, Quad5 9.5%, Quad6 6.7%, Quad7 3.4%, Liana Tangle 5.6%, Rav Palm 5 1.7%
Overall orientation: A 29.6%, B 66.5%, C 3.9%
Overall behaviors: Eat fruit 27.3%, Groom-self 3.9%, Move 14.5%, Rest 53.6%, Threat 0.6%
Total tree height: D 11.2%, E 57.5%, F 30.7%

Eulemur and *Hapalemur* were both observed to use this patch. *Eulemur* groups were the most common lemur found in this area, primarily feeding and resting in two famelona (*Chrysophyllum* sp.) trees that abut the longoza field. When fruit was no longer available these trees were still important resting areas and moving supports for the brown lemurs as they traveled through this patch to adjacent areas. When they moved, the lemurs often headed to the west using the smaller trees and low lying liana tangles lining the longoza field. Or the lemurs moved north towards the valley and then headed east before reaching the river, moving again through the low lying trees/shrubs and liana tangles adjacent to a smaller patch of longoza.

Fruit from the famelona tree were the only items eaten by the brown lemurs in this patch. The lemurs sat (61.2%) at a height of six meters or stood (34.6%) at a height of nine to ten meters on small (75.5%) oblique (89.8%) substrates to eat these fruits in quadrants three, four, and five (approximately 30%).

When moving in this area, the brown lemurs mainly used quadrupedal locomotion (53.8%) at a height of six to eight meters on small oblique substrates (76.9%). The quadrants used for moving were highly variable and the brown lemurs essentially used all areas of the canopy for movement. Leaping less than one meter (23.1%) was another form of movement in this patch and was conducted on small oblique substrates at a majority of the heights and quadrants. *Eulemur* groups were never observed to use or move through the longoza, but instead made use of the trees, low lying vegetation, the ground, and liana tangles to move around the longoza.

When resting, *Eulemur* individuals assumed their huddled tail wrapped position (71.9%) at a height of seven to eight meters (91.3%) on small horizontal (44.9%) and oblique (55.1%) substrates. When resting in this tail-wrapped position, *Eulemur* mainly used quadrant one. *Eulemur* also made use of quadrant four (57.1%) and liana tangles (38%) to sit and rest.

Summary of substrate use and total activity budget for *Hapalemur*:
Overall size of substrate: A 42.9%, B 57.1%
Overall height of substrate: A 100%
Overall quadrant: Quad7 71.4%, Liana 28.6%
Overall orientation: A 14.3%, C 85.7%
Overall behaviors: Move 28.6%, Rest 71.4%
Total tree height: A 14%, B 85.7%

While *Hapalemur* groups were observed moving through this patch, the sample size was small, consisting of a total of seven individuals. *Hapalemur* in contrast to *Eulemur*, moved directly through the longoza field vertical-clinging and leaping from one vertical support to the next. The group moved in a single line one waiting for, and following the next in line. *Hapalemur* individuals moved through the patch near plot 4 towards the smaller 100 m^2 patch of longoza between the forested areas. The bamboo lemurs also moved through a 100 m^2 longoza patch. The longoza stems used to move and periodically rest were small dbh, vertical substrates two meters in height. The bamboo lemurs also used small horizontal and vertical lianas to move and rest at a height of one meter.

PATCH ZUBENUBI
Summary of substrate use and total activity budget for *Indri*:
Overall size of substrate: B 19.8%, C 68.3%, D 11.1%, E 0.8%
Overall height of substrate: A 5.6%, B 55.6%, C 15.1%, D 3.2%, F 11.1%, H 9.5%
Overall quadrant: Quad3 0.8%, Quad5 8.7%, Quad6 13.5%, Quad7 76.9%
Overall orientation: B 79.4%, C 20.6%
Overall behaviors: Eat leaves 2.4%, Eat young leaves 8.7%, Groom-self 0.8%, Move 3.9%, Rest 82.5%, Kiss 1.6%
Total tree height: D 57.9%, F 21.4%, G 11.1%, I 9.5%

Indri groups that used this patch often approached from the northwest and moved right through continuing on to the east. All of the feeding behaviors occurred in the taller trees on the periphery of this patch and the adjacent area to this patch. This adjacent area had an overall

increase in canopy height as well as an increased number of larger dbh trees. This area also had an increase in plant composition diversity. While eating young leaves, indri assumed a sit-extend posture on medium, oblique substrates at a height of nine to ten meters in quadrant five (100%).

The sample size for indri moving through this patch was small (N=5). Given how fast they moved and their reluctance to linger in this patch, the indri were soon gone beyond the boundary of the patch so little behavioral data were collected. *Indri* moved by leaping one to four meters on vertical substrates in quadrant seven that ranged in size from small to large. The height of their movement also varied, ranging from one to three meters. The lianas in this patch form tangles at all levels and angles, creating essentially one closed prominent canopy layer starting from the ground and extending up to seven or eight meters masking much of the vertical space. On average, 110 lianas were counted per 100 m^2 although in some areas the number of lianas was as high as 158/100 m^2. Despite this cluttered vertical space, the indri had no problem negotiating their way through the open spaces using tree trunks and lianas along the way no matter how small the diameter of the substrate or the height.

While resting (11.5%) in the adjacent trees to the patch, indri individuals sat on medium, oblique branches in quadrant six at a height of four to five meters (33.3%) or twelve to thirteen meters (66.7%). While resting inside of the patch (87.5%) indri would vertically cling to small (25.6%), medium (61.1%), and large (12.2%), oblique (80%) or vertical (20%) substrates. Resting in the vertical-cling posture occurred in quadrant seven at various heights including at one meter (6.7%), two to three meters (75.6%), four to five meters (13.3%), and six or twelve to thirteen meters (2.2%).

Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: A 28.1%, B 59.6%, C 12.4%
Overall height of substrate: A 4.5%, B 13.5%, C 19.1%, D 20.2%, E 31.8%, F 19.6%
Overall quadrant: Quad1 3.9%, Quad2 7.3%, Quad3 4.5%, Quad4 12.4%, Quad5 23%, Quad6 1.7%, Liana Tangle 35.9%, Palm fruit 11.2%
Overall orientation: A 32.6%, B 75.9%
Overall behaviors: Eat fruit 37.1%, Eat leaves 9.6%, Move 20.2%, Rest 33.1%.

Total tree height: C 8.4%, D 9.6%, E 17.4%, F 44.4%

When eating fruit, *Eulemur* sat (63.1%) on very small (12.2%) or small (87.8%), horizontal (21.0%) or oblique (78.6%) substrates. *Eulemur* also stood (36.9%) on these same types of substrates to eat fruit. A variety of heights were used, although at varying frequencies. More time was spent at the taller heights of 9-13 (73.4%) and 6-8 (16.2%) meters with less time spent eating fruit at the lower heights of 2-3 (8.7%), 1 (1.2%), and 4-5 (0.6%) meters. In addition, *Eulemur* used a variety of quadrants to eat fruit with the main quadrants including the inside of liana tangles and sitting directly on top of the fruit clusters growing on palms. When eating leaves, the brown lemurs sat or stood an equal amount of time on small or medium oblique substrates. This behavior was primarily conducted at a height of seven to ten meters.

Eulemur mainly used quadrupedal locomotion (75%) when moving through this patch, although individuals would also occasionally leap less than one meter (22.2%). *Eulemur* generally used oblique (78%), small and medium sized substrates for all locomotion. Most *Eulemur* movement occurred at a height of four to six meters (72.2%). All quadrants were used for moving with an emphasized use of the liana tangles (61.1%) for within and between substrate movement patterns.

While resting, *Eulemur* used the tail wrap posture (71.2%) on small (69.0%), horizontal (38%), and oblique (61.9%) substrates. *Eulemur* rested at a height of seven to eight meters (49.1%) or nine to ten meters (22.0%) inside of liana tangles (18.6%), in quadrant four (22.0%), or quadrant five (49.2%).

PATCH BETAKONONA
Summary of substrate use and total activity budget for *Propithecus*:
Overall size of substrate: A 22.3%, B 28%, C 49.7%
Overall height of substrate: A 5.1%, B 1.7%, E 75.4%, F 17.7%
Overall quadrant: Quad2 17.7%, Quad3 13.7%, Quad4 8.6%, Quad5 24%, Quad7 8.6%, Liana Tangle 27.4%
Overall orientation: A 90.9%, C 9.1%
Overall behaviors: Eat leaves 15.4%, Move 4% (outside patch), Rest 60.6%, Groom-self 15.4%, Threat 4.6%

Total tree height: E 26.9%, F 68%, G 5.1%

The only feeding behavior observed among the sifaka using this patch was to eat the young red leaves of the mampay (*Cynometra* sp.) tree in October. The sifaka used a sit-extend posture (51.9%) or a recline posture (37.0%) but rarely a suspensory posture (11.1%) to eat the mampay leaves. Most of this leaf-eating took place on very small (77.8%), horizontal substrates at a height of seven to eight meters (100%) in quadrants three (51.9%), four (25.9%), and five (22.2%).

The sample size for sifaka moving behaviors is small (N=7) and occurred on the border and while leaving the patch. But out of these seven occurrences, the sifaka were observed to move primarily by two-meter leaps (57.1%) on medium, vertical substrates in quadrant seven at a height as low as one meter up to six to eight meters.

The majority of sifaka resting occurrences involved the sit-extend posture (98%) on very small (16.3%), small (19.2%), and medium (64.4%) sized horizontal substrates at a height of seven to eight meters (70.2%) or nine to ten meters (29.8%). The sifaka used a variety of different quadrants for resting with an emphasis on quadrant five (29.8%), quadrant two (29.8%), and lianas (19.2%). The lianas act as horizontal swings connecting different components of the canopy and tree trunks. While resting, sifaka would often self-groom. This grooming behavior made up 15% of their total activity budget.

Summary of substrate use and total activity budget for *Avahi*:
Overall size of substrate: A 5.5%, B 1.6%, D 92.9%
Overall height of substrate: B 1.6%, D 98.4%
Overall quadrant: Quad6 92.9%, Quad7 1.6%, Liana tangle 5.5%
Overall orientation: B 98.4%, C 1.6%
Overall behaviors: Eat leaves 22%, Groom other 1.6%, Groom-self 8.7%, Move 0.8%, Rest 66.9%
Total tree height: C 1.6%, 98.4%

Only one group, comprised of three *Avahi,* was observed in this patch. These individuals ate mampay leaves in quadrant six at a height of six meters in a seven-meter tree. Medium, oblique substrates were used. Feeding on leaves consumed 22% of their total time whereas 66.9% of their total time was spent resting.

While resting, the *Avahi* sat (98.8%) on medium, oblique substrates, at a height of six meters in quadrant six (91.7%) or within the liana tangles (8.3%) ensconcing the tree. The *Avahi* were active off and on in terms of grooming and eating from when they leapt into this patch at around 11:00 AM until 3:30 PM, at which point they left the patch and headed further west. This was an interesting observation given the primary nocturnal activity budget of these lemurs.

Summary of substrate use and total activity budget for *Indri*:
Overall size of substrate: A 7.1%, C 90.8%, D 2.0%
Overall height of substrate: E 43.9%, F 2.0%, G 16.3%, H 37.8%
Overall quadrant: Quad4 37.8%, Quad6 59.2%, Quad7 3.1%
Overall orientation: A 82.7%, B 14.3%, C 3.1%
Overall behaviors: Eat young leaves 9.2%, Groom other 2.0%, Groom-self 1.0%, Move 2.0%, Rest 85.7%
Total tree height: F 43.9%, I 56.1%

Indri spent most of their time resting (85.7%) in this patch. While resting, indri spent equal proportions in either a sit-extend (47.6%) or sit (51.2%) posture on medium, horizontal branches at a height of 7-8 meters (50%), 11 meters (19.0%), or 12-13 meters (28.6%). *Indri* primarily used quadrants 4 (29.8%) and 6 (69.0%) for resting.

In Patch Betakonona the indri were observed moving on only two occassions. One bout consisted of a three meter leap onto a large, vertical substrate at a height of eight meters. The other bout was a climb at a height of ten meters on a medium vertical substrate. When they engaged in between-substrate movement, they would vertically cling and leap off into the western portion of the reserve.

Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: A 48.5%, B 51.5%
Overall height of substrate: E 45.5%, F 45.5%, G 9.1%
Overall quadrant: Quad1 15.2%, Quad3 9.1%, Quad5 57.6%, Quad6 9.1%, Quad Liana 9.1%
Overall orientation: A 9.1%, B 87.9%, C 3.0%
Overall behaviors: Eat leaves 39.4%, Move 39.4%, Rest 3.0%, Threat 18.2%
Total tree height: E 9.1%, F 42.4%, G 48.5%

Eulemur primarily stopped and ate mampay leaves here, or the lemurs were moving through to another part of the forest when they were observed in patch Betakonona. *Eulemur*

rarely rested (3.0%) and never relaxed enough to groom themselves or others while in this patch. *Eulemur* were only observed to eat the young leaves of the mampay trees while standing on very small oblique substrates at a height of nine to ten meters (84.6%). The brown lemurs primarily used quadrant five while eating. Here, the brown lemurs were observed to have a ten meter group spread while eating the mampay leaves. For example, one group of brown lemurs that consisted of seven individuals divided such that two males and two females were in one tree eating one meter apart with three other males ten meters away in another mampay tree also eating leaves. In other patches, the brown lemur groups were observed to forage more closely together.

Eulemur used short leaps (<1 m) (30.8%) to move in and through this patch as well as quadrupedal locomotion (69.2%). Movement took place on oblique small substrates mainly at a height of seven to eight meters (69.2%). For moving, *Eulemur* mainly used quadrants five (53.8%), one (23.1%), and lianas (15.4%).

PATCH FARA
Summary of substrate use and total activity budget for *Varecia*:
Overall size of substrate: B 3.5%, C 73.7%, D 22.8%
Overall height of substrate: F 35.1%, H 8.8%, I 56.1%
Overall quadrant: Quad3 33.3%, Quad4 31.6%, Quad5 29.8%, Quad6 5.3%
Overall orientation: A 68.4%, B 31.6%
Overall behaviors: Move 21%, Rest 78.9%
Total tree height: I 43.9%, J 56.1%

While in patch Fara the ruffed lemurs were not observed feeding. *Varecia* moved mainly by quadrupedal locomotion (83.3%) with the occasional two meter leap (16.7%) on medium horizontal (58.3%) or oblique (41.7%) substrates in quadrant three (58.3%) at the heights ranging from ten to fifteen meters.

The ruffed lemurs rested primarily in a recline posture (91.1%) on medium and large horizontal (70.7%) and oblique (29.3%) substrates. The ruffed lemurs rested at a height of nine to ten meters (33.3%) or fourteen to fifteen meters (64.4%) in quadrants three (26.7%), four (37.8%), and five (26.7%).

Summary of substrate use and total activity budget for *Propithecus*:
Overall size of substrate: C 100%
Overall height of substrate: C 100%
Overall quadrant: 7 100%
Overall orientation: C 100%
Overall behaviors: Move 50%, Rest 50%
Total tree height: F 100%

A group of three sifaka was observed once in this patch. The sifaka moved through this area from the north and continued on to the south. The sifaka leapt in one to two meter bounds between medium vertical supports at a height of four meters. The sifaka also paused briefly in the vertical posture between leaps before moving on. As indicated by the percentages above, the behaviors were not variable.

Summary of substrate use and total activity budget for *Hapalemur*:
Overall size of substrate: A 89.4%, B 5.3%, C 5.3%
Overall height of substrate: A 7.4%, B 79.8%, C 7.4%, F 5.3%
Overall quadrant: Quad4 3.2%, Quad5 4.3%, Quad6 5.3%, Quad7 6.4%, Longoza 5.3%, Liana 75.5%
Overall orientation: A 78.7%, B 9.6%, C 11.7%
Overall behaviors: Move 19.1%, Rest 77.7%, Threat 3.2%
Total tree height: B 73.4%, C 13.8%, D 3.2%, E 4.3%, I 5.3%

Hapalemur moved through this area by quadrupedal locomotion (46.7%) and leaping less than one meter (20%) and one meter (33.3%), making use of very small (60%), small (26.7%), and medium (13.3%) substrates. When moving, the bamboo lemurs used oblique (53.3%) and vertical (33.3%) substrates at a range of heights varying from one to ten meters. *Hapalemur* also equally used a variety of different quadrants including four, five, six, seven, the longoza stems, and lianas.

When resting, the bamboo lemurs sat in the tail wrap posture a majority of the time (88.5%) at a height of two to three meters on horizontal, very small lianas. *Hapalemur* was not observed feeding while in this patch.

Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: A 23.2%, B 19.2%, C 34.3%, D 23.2%
Overall height of substrate: D 15.2%, E 2.0%, F 38.4%, G 3.0%, H 37.4%, I 4%

Overall quadrant: Quad1 9.1%, Quad2 3.0%, Quad3 18.2%, Quad4 16.2%, Quad5 45.5%, Quad6 7.1%, Quad7 1.0%
Overall orientation: A 63.6%, B 35.4%, C 1.0%
Overall behaviors: Move 37.4%, Rest 54.5%, Threat 8.1%
Total tree height: D 3.0%, E 12.1%, F 11.1%, G 26.3%, H 6.1%, I 36.4%, J 5.1%

Eulemur moved in patch Fara by quadrupedal locomotion (64.9%) and one meter leaps (27%) on very small (57.7%) and small (38.5%) horizontal (41.7%) or oblique (58.3%) substrates. *Eulemur* used all quadrants with an emphasis on quadrant three (43.2%). *Eulemur* also used all heights of the canopy, ranging from six meters up to fifteen meters, but the most frequent height used for movement was nine to ten meters (40.5%).

The predominant posture for *Eulemur* to rest in this patch was either a sit (44.4%) or a sit tail-wrap (42.6%) on medium (46.3%) or large (25.9%) substrates rather than very small or small substrates that were used for movement. The main quadrant for rest was quadrant five (74.1%) at the key heights of nine and ten meters (37.0%) or twelve and thirteen meters (44.4%) on horizontal (75.9%) or oblique (24.1%) substrates. *Eulemur* was not observed to eat while in this patch.

PATCH 800-900
Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: A 34.9%, B 45.9%, C 19.1%
Overall height of substrate: A 0.5%, B 22.4%, D 33.3%, E 31.1%, F 0.5%, G 12.0%
Overall quadrant: Quad1 1.1%, Quad2 19.7%, Quad3 15.8%, Quad4 9.3%, Quad 5 4.4%, Quad6 40.9%, Quad7 1.1%, Rav Palm4 1.1%, Palm 6 6.6%
Overall orientation: A 30.1%, B 68.3%, C 1.6%
Overall behaviors: Eat fruit 14.8%, Grooms-self 2.8%, Move 15.3%, Rest 65.0%, Threat 2.2%
Total tree height: B 9.8%, C 13.1%, D 22.4%, E 22.9%, F 19.7%, G 3.3%, H 8.7%

Eulemur often sat and ate fruit from the liana (85%) at a height of six meters (56.5%) and two to three meters (34.8%) in quadrant three (52.0%) and quadrant palm six (34.8%), on very small and small substrates. The lemurs took the outer spikey skin off the liana fruits with their teeth and then ate the fruit pulp inside of the husk.

Eulemur moved by one meter (17.9%) and two meter (7.1%) leaps as well as quadrupedal locomotion (75.0%) through a variety of heights from two to eleven meters. *Eulemur* also used a

number of quadrants in the canopy and trunk, but there was an emphasis on their use of quadrant three (57%). *Eulemur* used oblique substrates that were either very small (39.3%) or small (46.4%) for movement within this patch. The brown lemurs used ravinala leaves and palm leaves as the chosen substrate to move along, especially where these substrates formed a continuous lemur highway. *Eulemur* typically moved at a height of five meters in the continuous vegetation moving through quadrants three, four, and then three again of the adjacent tree.

Eulemur rested in a sit tail-wrap posture (89.1%) primarily at the heights of six meters (34%) or seven and eight meters (41.5%), but also at a height of eleven meters (17.9%). The brown lemurs rested in quadrant two (30.2%), splitting their time between horizontal (49.1%) or oblique (50.9%) very small (33.6%), small (41.2%), or medium (25.2%) substrates.

Summary of substrate use and total activity budget for *Propithecus*:
Overall size of substrate: B 82.4%, C 17.6%
Overall height of substrate: A 17.6%, B 52.9%, C 11.8%, D 11.8%, E 5.9%
Overall quadrant: Quad6 41.2%, Quad7 58.8%
Overall orientation: B 44.1%, C 55.9%
Overall behaviors: Mark 5.9%, Move 20.6%, Rest 58.8%, Threat 14.7%
Total tree height: D 61.8%, E 2.9%, F 29.4%, H 5.9%

Two sifaka were observed marking trees in this patch as they moved through and towards the west. The female urine marked and the male followed marking with his sternal gland, sometimes biting into the bark to create a depression before rubbing the area. The male was following the female, overlaying his scent onto hers. This group of two moved and marked the trees in the western portion of the patch and crossed over the main trail at 1000 meters, continuing their travel to the west outside the boundary of the patch. The sifaka leapt distances from one to four meters in quadrant seven on vertical substrates at variable heights ranging from one meter to eight meters.

While resting, the sifaka assumed a sit-extend posture (65%) on small oblique substrates in quadrant six at a height of two to three meters. The sifaka were not observed to eat food while using this patch.

Summary of substrate use and total activity budget for *Hapalemur*:
Overall size of substrate: A 64%, B 8%, C 28%
Overall height of substrate: A 44%, B 12%, C 44%
Overall quadrant: Quad7 60%, Bamboo cluster 16%, Liana tangle 20%, Palm6 4%
Overall orientation: A 4%, B 36%, C 60%
Overall behaviors: Eat leaves 40%, Move 28%, Rest 24%, Threat 8%
Total tree height: A 16%, C 32%, D 52%

Hapalemur ate leaves from a cluster of bamboo and viney liana tangle while vertical-clinging to very small, oblique and vertical substrates one meter in height while in this patch.

Hapalemur moved by leaping one to three meters on small and medium vertical substrates at a height of two to five meters. When resting, the bamboo lemurs would vertically cling to very small, and in some cases medium, oblique and vertical substrates. Resting occurred at a height ranging from one to three meters in quadrant seven or within the liana tangles.

PATCH SAHAKOHO
Summary of substrate use and total activity budget for *Eulemur*:
Overall size of substrate: A 42.9%, B 55.7%, C 1.4%
Overall height of substrate: D 1.4%, E 52.9%, F 45.7%
Overall quadrant: Quad1 1.4%, Quad4 45.7%, Quad5 22.9%, Quad6 30%
Overall orientation: A 57.1%, B 42.9%
Overall behaviors: Move 24.3%, Rest 75.7%
Total tree height: E 42.9%, F 57.1%

Eulemur moved (24.3%) and rested (75.7%) in this patch but were not observed to feed. *Eulemur* primarily used quadrupedal locomotion (82.4%) while moving in this patch and only occasionally leaping one or less than one meter. *Eulemur* used very small and small substrates in quadrant five for movement. The brown lemurs moved at a height of seven to eight meters on horizontal (47%) and oblique (52.9%) substrates.

While resting, the brown lemurs assumed a sit (60.4%) or sit tail wrap posture (39.6%) on very small (39.6%) or small (60.4%) horizontal (60.4%) or oblique (39.4%) substrates. Resting took place at a height of seven to eight meters (39.6%) or nine to ten meters (60.4%) in quadrant four or six.

Summary of substrate use and total activity budget for *Indri*:
Overall size of substrate: B 51.2%, C 44.2%, D 4.7%
Overall height of substrate: A 9.3%, B 2.3%, C 2.3%, E 39.5%, F 44.2%, H 2.3%
Overall quadrant: Quad4 9.3%, Quad6 20.9%, Quad7 69.8%
Overall orientation: A 25.6%, B 37.2%, C 37.2%
Overall behaviors: Eat leaves 4.7%, Groom-self 4.7%, Kiss 23.3%, Move 20.9%, Rest 46.5%
Total tree height: C 6.9%, F 16.3%, G 34.9%, I 41.9%

Indri was primarily moving through or resting while in this patch with very little feeding behavior. Leaping consisted of one to three meter vertical leaps on vertical substrates in quadrant seven. *Indri* individuals moved at variable heights ranging from one to ten meters on small (44.4%), medium (44.4%), and large substrates.

While resting, indri used sit (80.0%), suspensory (5.0%), and vertical clinging (15.0%) postures at the heights of seven to eight meters (65.0%) and nine to ten meters (35.0%) mainly in quadrants six (30.0%) and seven (65.0%). *Indri* used horizontal (30.0%), oblique (50.0%), and vertical (20.0%) substrates that were either small (65.0%) or medium (35.0%) in size.

Summary of substrate use and total activity budget for *Propithecus*:
Overall size of substrate: B 62.7%, C 27.2%, D 10.2%
Overall height of substrate: C 37.3%, E 62.7%
Overall quadrant: Quad6 66.1%, Quad7 33.9%
Overall orientation: A 30.5%, B 54.2%, C 15.3%
Overall behaviors: Eat young leaves 30.5%, Move 3.4%, Rest 66.1%
Total tree height: D 18.6%, F 18.6%, G 62.7%

Propithecus ate young leaves in a vertical-cling posture on small, oblique substrates at a height of seven to eight meters in quadrant six. Sifakas were seen locomoting only twice in this patch. On both occurrences the sifaka leapt two meters onto medium vertical substrates at a height of four to five meters in quadrant seven.

Resting occurred in a sit (74.3%) or vertical-cling (25.6%) position on small (48.7%), medium (35.9%), or to a lesser extent, large (15.4%) substrates. The substrates used were horizontal (46.2%), oblique (35.9%), or vertical (17.9%) at the heights of four to five meters (51.3%) or seven to eight meters (48.7%) in quadrant six (53.8%) or quadrant seven (46.2%).

ANALYSIS BY LEMUR TAXON

The following descriptions address in more detail the questions presented at the beginning of this chapter. These descriptions help to understand how different levels of spatial scale (macro- and micro-habitat features) affect lemur community structure.

Eulemur fulvus albifrons

Eulemur utilized all eight of the quantified patches in BNR. However, *Eulemur* groups spent more time in certain patches than others (Figure 5.1). These more frequented patches included 1600 (21%), 800-900 (16%), Guava (16%), Zubenubi (15%), and Sahabefoza (15%)[9] (Figure 5.1). The least amount of time was spent in Patch Betakonona (Figure 5.1). There were also differences in the percentage of time dedicated to the different observed behaviors recorded via the point counts within the patches (e.g. in certain patches brown lemurs may focus more of their time on eating and less time on resting, whereas in other patches brown lemurs may spend more time moving and less time resting) (χ^2=178.8, df=14, p<0.001). Specifically, within the most frequented patches, rest was the primary behavior. The guava patch is the only exception, where brown lemurs spent equal amounts of time resting and moving (Figure 5.2). In Patch 1600, they spent equal percentages of their time eating and moving with more time resting (Figure 5.2). In Patch Guava, the brown lemurs spent equal amounts of time moving and resting and less time eating (Figure 5.2). In Patch 800-900, they spent equal amounts of time eating and moving with a much higher percentage of time dedicated to resting. In Patch Zubenubi, the brown lemurs spent a majority of their time eating, followed by resting, and then moving. In Patch Sahabefoza, the brown lemurs spent the most time resting followed by eating and then moving (Figure 5.2).

[9] Percentages are based on the total number of behaviors of all the *Eulemur* groups observed in each patch.

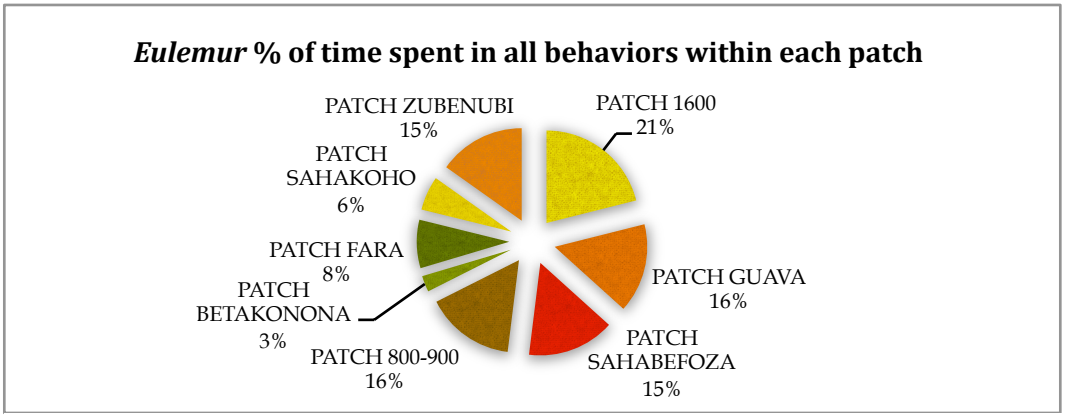


Figure 5.1 *Eulemur* total percentage of time engaged in all behaviors in each patch

Why are brown lemurs resting so much in Patch 800-900?

In a comparison based on percentages calculated from the total sum of *Eulemur* behaviors from all the patches (Figure 5.3), brown lemurs rested a higher percentage of their time in Patch 800-900, fed a higher percentage of their time in Patch Zubenubi, and moved a high percentage of their time in Patches 1600 and Guava. Why were brown lemurs resting the most in Patch 800-900? An analysis of posture and substrate use reveals that *Eulemur* rested in a sit tail-wrap posture

Table 5.1 *Eulemur* counts dedicated to different behaviors based on sums from all the patches

	PATCH							
BEHAVIOR	1600 (N)	GUAVA (N)	SAHABEFOZA (N)	800/900 (N)	BETAKONONA (N)	FARA (N)	SAHAKOHO (N)	ZUBENUBI (N)
EAT	50	35	49	27	13	0	0	83
MOVE	52	59	26	28	13	37	17	36
REST	87	58	96	119	1	54	53	59

(89.1%) primarily at the heights of six meters (34%) or seven and eight meters (41.5%) while in Patch 800-900. The brown lemurs rested in quadrant two (30.2%), splitting their time between horizontal (49.1%) or oblique (50.9%), very small (33.6%), small (41.2%), or medium (25.2%) substrates. Patch 800-900 has one of the highest average abundances of liana (25/100 m^2) and

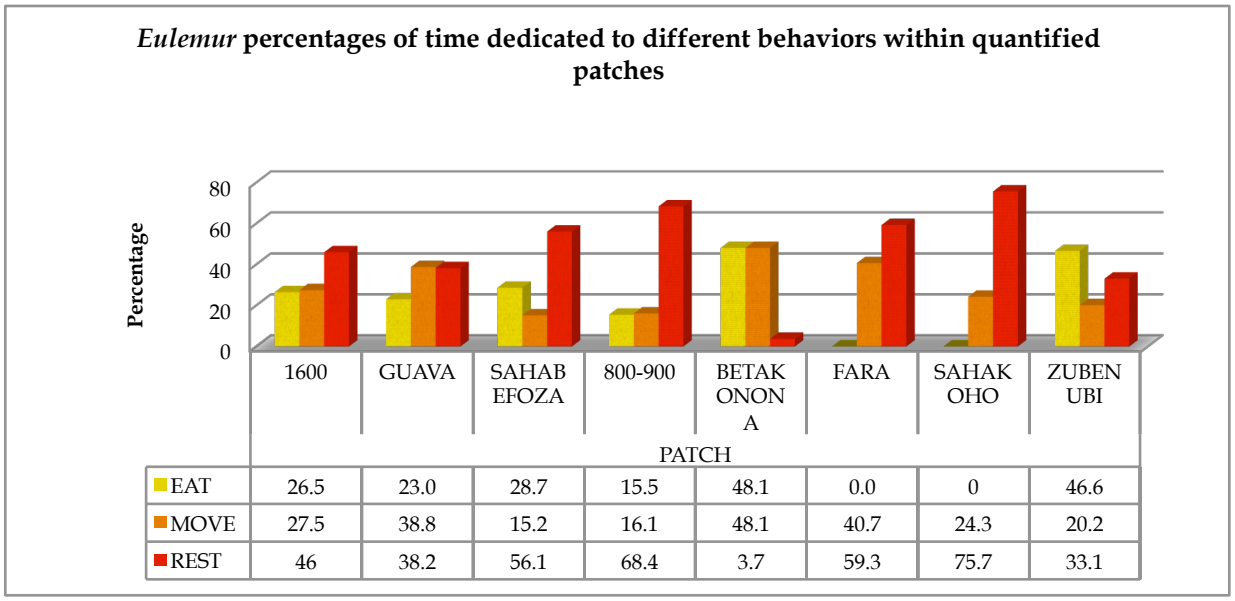


Figure 5.2 *Eulemur* percentages of time dedicated to different behaviors within quantified patches

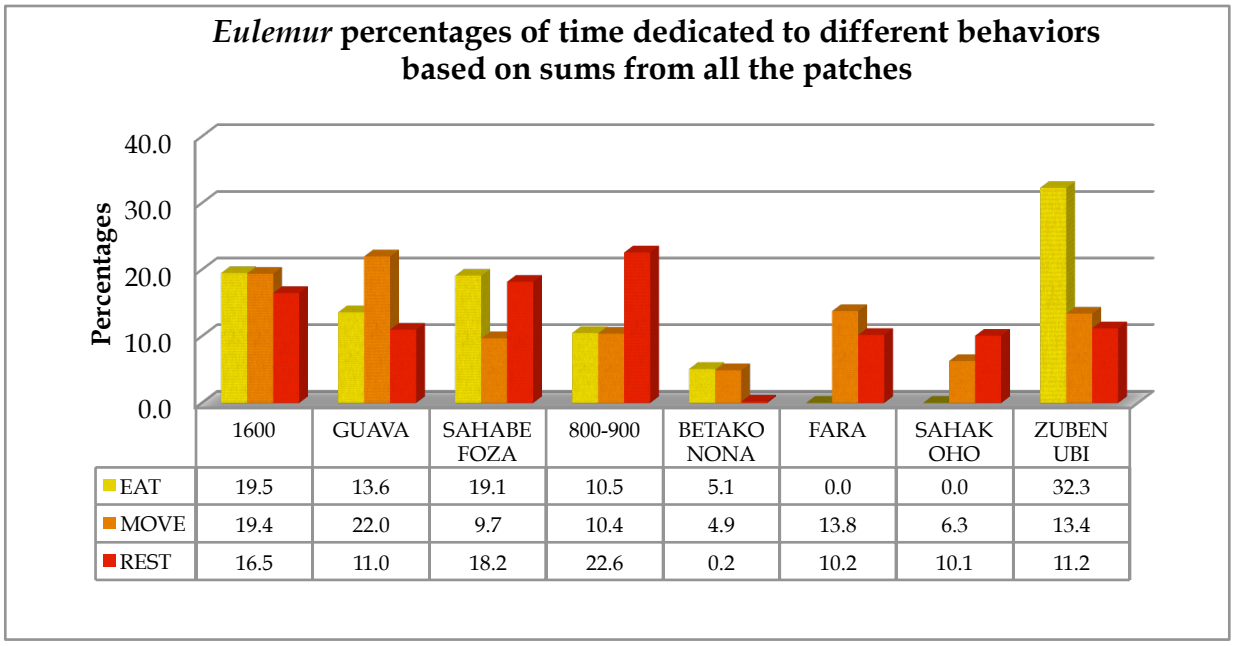


Figure 5.3 *Eulemur* percentages of time dedicated to different behaviors based on sums from all the patches

dead standing and fallen trees cluttering much of the horizontal and vertical space. Patch 800-900 also has a high density of 1-5 cm and 6-10 cm dbh trees, further contributing to the closed nature of this patch. Overall canopy height is also relatively low. Keystone features (*sensu* Tews et al., 2004) in this patch that may influence the higher percentage of resting behaviors are favored ramy trees that are ensconced in lianas, providing a protective cryptic refuge. Several different groups of *Eulemur* were observed using these structures for rest and grooming social interactions.

The patch where the least amount of resting was observed was Betakonona. Patch Betakonona has a high abundance of equally ≤1 meter spaced 1-5 cm dbh trees similar to Patch 1600, but the abundances of liana and dead trees are much lower in comparison to Patch 800-900. Patch Betakonona, in contrast to Patch 800-900, has one of the tallest canopy heights, with the height of canopy layer three being the tallest among the patches. Canopy layers one and two are connected, but the generally taller canopy height gives this patch more open space. There are no ravinala palms here, whereas Patch 800-900 has some of the highest abundances of these palms. *Eulemur* actively used ravinala palms when they were available and a lack of them in an area might have influenced their patch choice. Patch Betakonona contains seven ramy trees, but these trees have not been taken over by dense understory and lianas like those trees in Patch 800-900. Perhaps favored sleeping sites within a patch influence brown lemur preferred use of certain patches.

Why are brown lemurs feeding the most in Patch Zubenubi?

Brown lemurs engaged in feeding behaviors the most in Patch Zubenubi, whereas no feeding behavior was observed in Patches Fara and Sahakoho. Why is this? Is it the substrates? Is it food availability? Furthermore, what substrates did brown lemurs feed on in Zubenubi and are these different than what is available in Fara and Sahakoho? To answer these questions, a comparison was made of the substrates and plant composition of Patch Zubenubi with that of Fara and Sahakoho. *Eulemur* was primarily eating fruit (and some leaves) of liana and hazomainty

(*Diospyros* sp.) while in Patch Zubenubi. When eating fruit, *Eulemur* sat (63.1%) on very small (12.2%) or small (87.8%), horizontal (36.1%) or oblique (63.9%) substrates. *Eulemur* also stood (36.9%) on these same types of substrates to eat fruit. A variety of heights were used, including one meter (9.6%), two to three meters (25.3%), four to five meters (13.3%), six meters (19.3%), seven to ten meters (33.7%). In addition, *Eulemur* used a variety of quadrants to eat fruit, with the main quadrants being the inside of liana tangles and sitting directly on top of the fruit clusters growing on palms. Lianas had the highest average abundance per 100 m^2 in Patch Zubenubi, perhaps attracting the brown lemurs to this area to consume the fruits. Hazomainty was one of the most abundant tree taxa that occurred in this location (19/patch), the fruits of which the brown lemurs also eat. At first glance, Zubenubi appeared like a viney degraded mess, but upon further investigation this is an important foraging area for various brown lemur groups.

Patch Fara had the lowest abundance of lianas as well as a low abundance of hazomainty trees. Hasina keliravina (*Dracaena reflexa*) were the most abundant tree taxon in Patch Fara. I did not observe the brown lemurs to eat from these trees during this research time period, which is not to say these trees are unimportant, but rather that the extent of their influence prompts further investigation. Fara also had ample open space both vertically and horizontally in the understory. Fara was the only patch to have small gaps within the first canopy layer with the taller layers exhibiting more connectivity. Although brown lemurs did not consume foods here, they were observed to rest in Patch Fara on medium (46.3%) or large (25.9%) substrates rather than the very small or small substrates that brown lemurs frequently used in other patches, indicating that they will use these larger substrates. Not only were brown lemurs using larger substrates, they also utilized taller heights of the canopy. For example, the main quadrant for rest in Patch Fara was quadrant five (74.1%) at the key heights of nine and ten meters (37.0%) or twelve and thirteen meters (44.4%) on horizontal (75.9%) or oblique (24.1%) substrates. Perhaps the lack of understory/canopy congestion or lack of favored food trees is a deterrent to brown lemur groups.

Moreover, the favored food trees of brown lemurs may have not been in bloom during the course of this research, underestimating the importance of this patch. Brown lemurs also had a higher overall abundance in Patch 800-900 than in Patch Fara, which may influence the use patterns among brown lemur groups and thus the results of this research.

The most abundant trees in Patch Sahakoho included lalotina (*Anthostema madagascariensis*). There were also seven hazomainty trees, trees that were important to the brown lemurs in Patch Zubenubi. The abundance of 1-5 cm dbh trees was moderate-to-high in comparison to the other patches but the densities of 6-10 cm, 11-20 cm, and 21+ cm dbh trees were the highest in this patch in comparison to the other patches. The quantified patch area also had the lowest abundance of lianas, dead trees, and herbaceous new growth on the forest floor, allowing for open vertical and horizontal space. In contrast, the area to the west of this patch had increased amounts of guava, tree falls, and ravinala palms all of which continued to increase as one moved closer to the forest edge. This area also had a lower two to four meter tall, connected layer that formed tunnels of vegetation in some sections. Dead fallen ravinala palms further contributed to the dense understory. Brown lemurs were observed to frequent this adjacent patch, perhaps eating their fill here and then moving into the Sahakoho Patch for rest. In the future, more focus will be given to this western adjacent patch and *Eulemur* feeding behavior.

What Patches Promote Movement?

Brown lemurs moved the most in Patches 1600 and Guava and the least in Betakonona. What about these patches promotes movement? Alternatively, is there something about the substrates in Patch Betakonona that hinder movement? In the guava, the brown lemurs had a range of locomotor modes. These included bridging, leaping ≤1 meter, and quadrupedalism. The brown lemurs moved mainly by quadrupedal locomotion (66%) and less by leaping short distances (<1 m) (19%). When moving quadrupedally or leaping short distances, the brown lemurs traveled at a height of one meter (72%) on oblique, very small (<1 cm dbh) substrates (90%). When

moving, the brown lemurs would proceed primarily through the thickest parts of the guava (42%), traveling at a height of 1 meter on very small substrates. The brown lemurs also used ravinala and palm leaves as chosen substrates to move along, especially where these substrates formed continuous lemur highways. In Patch 1600, the brown lemurs used several forms of locomotion, including leaping ≤1 meter, leaping in two meter increments, and quadrupedalism, although the primary means of moving was quadrupedal locomotion (71%) with the occasional leap of ≤1 meter. Very small and small sized substrates were most commonly used. *Eulemur* used oblique branches for quadrupedal locomotion, and when leaping, individuals used all orientations, although longer distance leaps of one or two meters were often made on vertical supports. The main quadrupedal movement was at a height between six and eight meters. Leaping occurred within a wider range of heights between two and ten meters.

In Patch Betakonona, the brown lemurs moved by quadrupedalism (69.2%) and short leaps (<1 m) (30.8%) through the connected portions of the canopy. Movement took place on oblique small substrates mainly at a height of seven to eight meters (69.2%). For moving, *Eulemur* mainly used quadrants five (53.8%), one (23.1%), and lianas (15.4%). *Eulemur* moved through the connected portions of the canopy, using quadrant five of the trees where the branches touch and create a continuous pathway.

The brown lemurs appeared to be quite flexible in their ability to utilize multiple forms of locomotion on varying sized substrates of different heights. Brown lemurs ate and rested here more than any movement behaviors. While in Patch Betakonona, the lemurs were mainly eating mampay leaves. These leaves are abundant and do not require much movement within the tree to feed. The leaf distribution perhaps limited the need to move in the patch. Conceivably, brown lemurs were attracted to this patch to eat the abundant mampay leaves, directing more focus to eating and resting and not moving. After the brown lemurs were finished eating the mampay leaves, perhaps the movement process to the next patch was what was important and not

locomoting while in the patch. An artifact with focal animal sampling at two minute intervals is that one only records the behavior observed on the two minute mark. If locomoting occurred before or after this "snap-shot" of time then it is not recorded. A small sample size and limited number of observations may only represent a fraction of the total activity budget. The lower amount of moving behavior recorded may be do to the low abundance of brown lemurs that occupied Betakonona, especially in comparison to Patches 1600 and Guava.

Within-Substrate and Between-Substrate Movement

Another interesting topic for understanding different movement patterns within the patch includes an analysis of locomotor modes and the vegetative quadrants used for within-substrate[10] movement versus between-substrate movement. This is important in the context of connectivity. There are different types of movement. Some habitat may be associated with short-range foraging, whereas other habitat types might promote long-distance movement patterns (e.g. Johnson et al., 2002). Movement within a tree while feeding and foraging differs from that of travel (Fleagle and Mittermeier, 1980; Gebo, 1992; Dagosto and Yamashita, 1998). For example, quadrupedalism and climbing are more frequent within-tree movement. Further, larger food trees provide an opportunity to spend more time in a single food patch and less time traveling (Strier, 1987). If lemur movement within a substrate is different from between tree movement, then this becomes important in building forest corridors or reforestation efforts within the forest itself, if the goal is to improve dispersal or increase lemur mobility. Movement within a tree while an animal is foraging often differs from positional behavior during travel (Fleagle and Mittermeier, 1980). In addition, larger food trees provide the opportunity for an animal to delegate increased time to foraging in a single tree and less time moving between feeding patches (Strier, 1987). Sampling more within-tree movement could influence the overall locomotor behavior results.

[10] A substrate may include a tree, shrub, liana, vine tangle, etc.

In Patch 1600, the brown lemurs used between-substrate movement 58.5% (N=31) and within-substrate movement 41.5% (N=22) of the time out the total number of locomotor bouts. Between-substrate movement included <1 to 2 meter leaps (N=12). For between-substrate movement, the brown lemurs used quadrant three (N=3) for leaps of <1 m and quadrant seven for one and two meter leaps (N=5). For quadrupedal locomotion, the brown lemurs used a variety of quadrants but focused on quadrant three (N=7) and the use of lianas (N=12). Within-substrate movement consisted primarily of quadrupedal locomotion (N=19). For within-substrate movement, the brown lemurs used quadrants four and five for short leaps <1m (N=3) and mainly quadrants three and four (N=11) for quadrupedal locomotion.

In Patch Guava, the brown lemurs used between-substrate movement 55.0% (N=33) and within-substrate movement 45% (N=27) of the time. Between-substrate movement consisted mainly of ≤1 meter jumps (N=16). For between-substrate movement, the brown lemurs used short leaps of <1m in the guava (N=5) and 1 meter leaps in quadrant 7 (N=3). The brown lemurs also used the guava thickets for quadrupedal locomotion (N=11). Within-substrate movement consisted of quadrupedalism (N=23) and the rare ≤1 meter jump (N=4). For within-substrate movement, the brown lemurs used the guava thickets for small leaps (<1m) (N=2) and for quadrupedal locomotion (N=17). The brown lemurs used ravinala palms for leaps of 1 meter (N=2).

In Patch Betakonona, the brown lemurs used between-substrate movement 69.2% (N=9) and within-substrate movement 30.8% (N=4) of the time. For between-substrate movement, the brown lemurs used short leaps (<1m) (N=4). The use of quadrants for between-substrate movement included the use of lianas (N=2) for leaps <1 m and quadrant five for quadrupedal locomotion (N=3).

For within-substrate movement, the brown lemurs used quadrupedalism (N=4) primarily in quadrant five (N=3). The brown lemurs also used quadrant one for 1 meter leaps (N=1).

Summary of Brown Lemurs

In sum, the brown lemurs used all of the quantified patches in BNR. Brown lemurs had a heightened preference for certain patches compared to the others as well as engaging in certain behaviors at a higher frequency in some patches compared to others (χ^2=178.8, df=14, p<0.001). For resting behaviors, brown lemurs sought out specific sleeping trees as described above in Patch 800-900 that may influence the predominant use of one patch over another. Patch choice may also be influenced by the plant composition of the patch and available food resources. Primates spend a majority of their day foraging for food, so food availability is certainly a factor at some level for patch choice. Brown lemurs moved a higher percentage of time in Patches 1600 and Guava, especially in comparison to Patch Betakonona where the lowest overall percentages of movement were observed. For a more meaningful analysis of the movement observations, the movement patterns were grouped into within-substrate and between-substrate categories. Brown lemurs in Patch 1600 used between-substrate movement a higher percentage of the time. The brown lemurs were capable of jumping up to two meters while using quadrant seven, although quadrupedal locomotion in the canopy using quadrant three or lianas was more frequent. For within-substrate movement, the focus was on quadrupedal locomotion in quadrants three and four and short leaps (<1 m) in quadrants four and five. In Patch Betakonona, the brown lemurs also used between-substrate movement more frequently. For between-substrate movement, the brown lemurs used short leaps (<1 m) onto lianas that connected the horizontal space. For quadrupedal locomotion, the brown lemurs used quadrant five. Within-substrate movement was primarily in the form of 1 meter leaps in quadrant one.

In all three patches the brown lemurs used between-substrate movement more frequently. For greater distance leaps (>1 m) the brown lemurs used the vertical trunks of trees in the guava or 1600 patch. The brown lemurs were not observed to make these longer distance leaps within Patch Betakonona using vertical tree trunks. Instead, the brown lemurs made use of lianas. The

understory of Betakonona is rather open in comparison to the more congested nature of Patches 1600 and Guava. Brown lemurs may assess their movement patterns by the amount of liana and understory growth and tree falls as elements of safety in planning their movement paths. This is supported by the variety of different brown lemur locomotor positions in the guava and 1600 patch compared to Betakonona. Perhaps the brown lemurs were limited due to the feeling of exposure and primarily concentrated their movement paths on the connected canopy, which can be used as an arboreal highway.

Overall, *Eulemur* was found within patches that contain features that are often associated with "degraded" forest. These features include abundant tree falls covered in viney bamboo or mazomboty that create congestion in the understory, trees that are shade intolerant and germinate in light gaps (e.g. ravinalas), and invasive species. *Eulemur* had an affinity for areas with abundant liana and vine tangles that form dense thickets in the upper canopy or lower understory. The abundance and diversity of lianas has been observed to increase in areas of disturbance (Laurance et al., 2001) as well as in areas between old growth and secondary forests (DeWalt et al., 2000). Lianas have the capacity to produce many rooting stems and therefore can colonize disturbed areas quite rapidly (Schnitzer and Bongers, 2002). *Eulemur* used these dense liana thickets both as a food source, consuming the leaves and the fruits, and as a safe refuge for resting behaviors. *Eulemur* also made use of individual lianas that bridged the gap in open parts of the canopy as important moving substrates. Lianas appear to be important food resources and pathways for brown lemurs, behaviors which have also been observed in other forest-dwelling animals (Emmons and Gentry, 1983; Chiarello, 1994; Preece, 2006; Martins, 2009).

Eulemur also used patches that were adjacent to large expanses of longoza fields even though this macrohabitat feature contributes to a lack of connectivity across the landscape. *Eulemur* were also found in areas of primary forest (e.g. Fara) and transition forest areas (e.g. 800-

900). This may indicate that macrohabitat and perceived boundaries of the landscape do not affect brown lemurs in BNR.

The above discussion and analysis addresses how brown lemurs express intra-species differences in behaviors within the quantified patches, further providing support for the behavioral and ecological flexibility observed within the genus *Eulemur*. This plasticity may also account for the consistent higher abundance of brown lemurs throughout the patches in BNR in comparison to the other diurnal lemur taxa.

Propithecus diadema diadema

Propithecus utilized five out of the eight quantified patches and some were used more frequently than others (Figure 5.4). These more frequented patches included Betakonona (62%), Sahakoho (21%), and 800-900 (12%). The least amount of time was spent in Patches Fara and 1600 (Figure 5.4). There were also differences in the percentages of time dedicated to the different observed behaviors recorded via the point counts within the patches (χ^2=110.8, df=6, p<0.001)[11]. Specifically, within the most frequented patches, the primary behavior was rest, although time dedicated to moving and resting was variable. In Patch 800-900 the sifaka spent no time feeding, but time was dedicated to moving. In contrast, in Patch Betakonona time was dedicated to eating but not moving (Figure 5.5, Table 5.2). Finally, in Patch Sahakoho more time was dedicated to eating rather than moving (Figure 5.5).

In a comparison based on percentages calculated from the total sum of *Propithecus* behaviors from all the patches (Figure 5.6), sifaka move the most in Patch 800-900 (77.8%) with no movement within Patch Betakonona. While there was no movement in Patch Betakonona, *Propithecus* ate the most here relative to the other patches. Sifaka also rested the most in Patch Betakonona (63.1%) and the least in 800-900 (11.9%). Why were sifaka resting and eating the

[11] Patch Fara was removed from the statistical analysis because there was only a count of three in this patch, making this too small of a sample size for Chi-square.

most in Patch Betakonona? Why were the sifaka not foraging in Patch 800-900, but engaged in the most movement here? To answer these questions a comparison was made of the substrates and plant composition of the most frequented patches in addition to the posture and substrate use used by *Propithecus*.

Why are sifaka resting and feeding the most in Patch Betakonona?

In Patch Betakonona the majority of sifaka resting occurrences involved the sit-extend posture (98%) on very small (16.3%), small (19.2%), and medium (64.4%) sized horizontal substrates at a height of seven to eight meters (70.2%) or nine to ten meters (29.8%). The sifaka used a variety of different quadrants for resting with an emphasis on quadrant five (29.8%), quadrant two (29.8%), and lianas (19.2%). The lianas act as horizontal swings connecting different components of the canopy and tree trunks. While resting, sifaka would often self-groom. This grooming behavior made up 15% of their total activity budget while in patch Betakonona. In Patch 800-900, while resting the sifaka assumed a sit-extend posture (65%) on small oblique substrates in quadrant six at a height of two to three meters. The sifaka appeared to demonstrate more flexibility in their resting behaviors in Patch Betakonona than in Patch 800-900. Patch 800-900 is the transitional area from non-primary/ "degraded" habitat to areas consisting of more primary forest. As such, this patch has an eclectic range of different vegetative attributes to also accommodate such flexibility. A favored specific tree was not observed other than the preference for quadrant six (i.e. lowest part of the canopy closest to the trunk) on small substrates. This vegetative attribute is common throughout many patches and is not patch specific to 800-900. In Patch 800-900, other correlated behaviors as part of the total activity budget were recorded that were not observed among the sifaka in Patch Betakonona. For example, sifaka in Patch 800-900 devoted more time to marking (5.9%) and threatening (the researcher) (14.7%) than the sifaka in Patch Betakonona where no marking was observed and less time was devoted to threats (4.6%).

Also, in Patch Betakonona the sifaka spent some time out of their total activity budget self-grooming (15.4%). No grooming was observed among the 800-900 sifaka. The sifaka using Patch 800-900 were much closer to the reserve edge and might experience more anthropogenic threats such as hunting. Therefore, these sifaka were "on the go" as they move through this patch with little time to rest. The sifaka in Patch Betakonona appeared to be more relaxed and spent more time resting, grooming, and feeding.

This line of reasoning could also be applied to why the sifaka were eating in Betakonona and not in Patch 800-900. The feeding behavior observed among the sifaka using patch Betakonona was the consumption of young red leaves of the mampay tree. The sifaka used a sit-extend posture (51.9%) or a recline posture (51.9%) but rarely a suspensory posture (11.1%) to eat the mampay leaves. Most of this leaf-eating took place on very small (77.8%), horizontal substrates at a height of seven to eight meters (100%) in quadrants three (51.9%), four (25.9%), and five (22.2%). Due to the seasonal nature of eating these leaves, the amount of time feeding in this patch compared to others may be overestimated and long-term research is needed to answer more effectively the influence of seasonal foods on patch use and heterogeneity. Ten mampay trees were counted in Patch 800-900 and thus were available for consumption. The hurried state of the sifaka through this patch gave them little time to eat, which may be an artifact of being unhabituated to the researcher or because of heightened vigilance due to previous hunting pressure. Sifaka were quick to notice humans in the vicinity, whereas *Eulemur*, as described in the previous section, may not notice human presence for a period of 45 minutes indicating the sifakas' higher degree of environmental awareness.

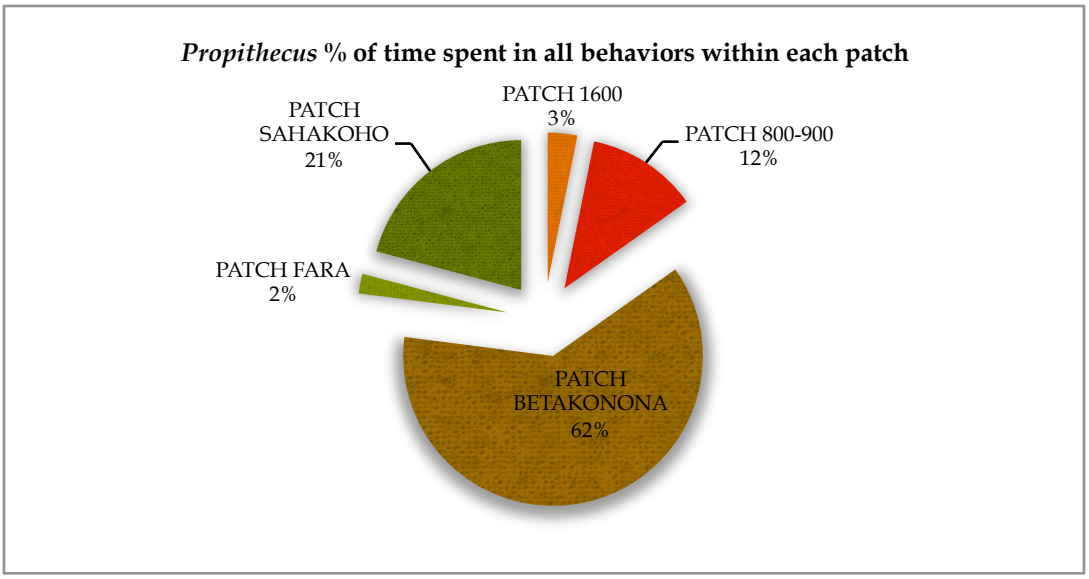


Figure 5.4 *Propithecus* groups total percentage of time engaged in all behaviors in each patch

Table 5.2 *Propithecus* counts of different behaviors within quantified patches.

	PATCH				
BEHAVIOR	1600 (N)	800-900 (N)	BETAKONONA (N)	FARA (N)	SAHAKOHO (N)
EAT	9	0	27	0	18
MOVE	0	7	0	0	2
REST	0	20	106	3	39

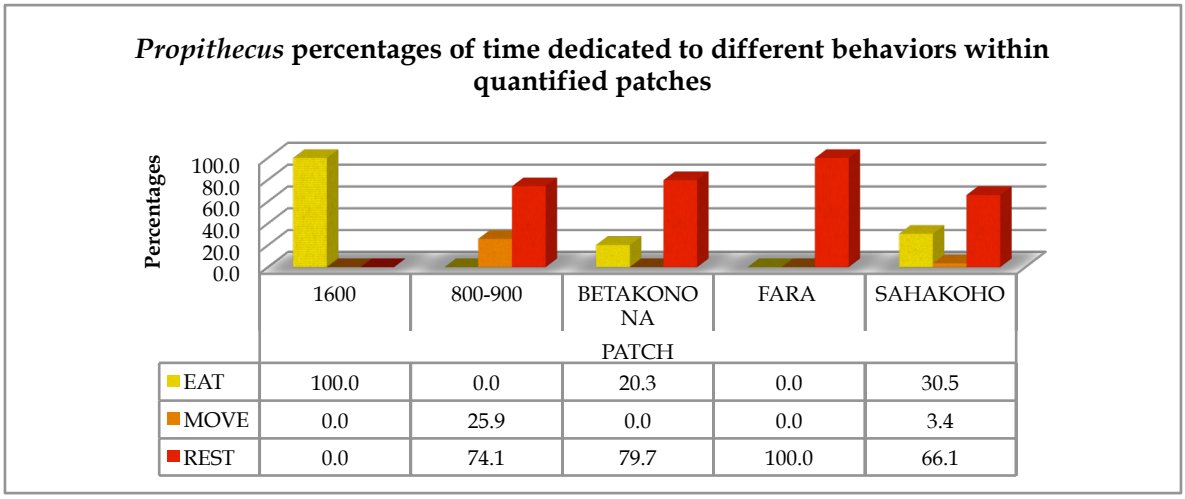


Figure 5.5 *Propithecus* percentages of time dedicated to different behaviors within quantified patches

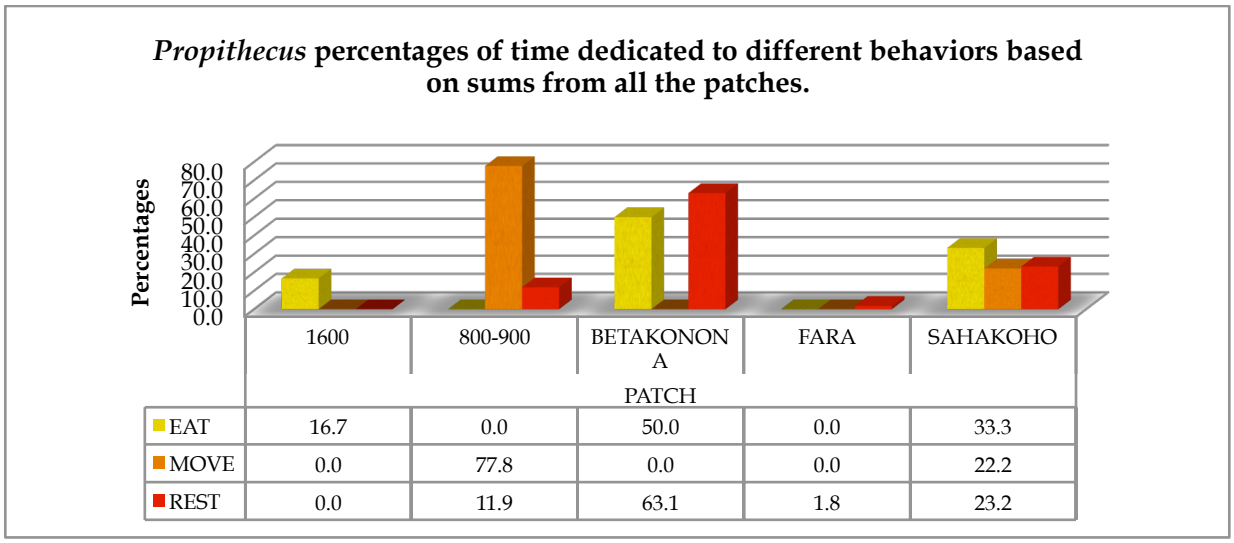


Figure 5.6 *Propithecus* percentages of time dedicated to different behaviors based on sums from all patches

Why were the sifaka not foraging in Patch 800-900 but engaged in the most movement here?

Propithecus moved in Patches 800-900, and to a lesser extent Sahakoho, but no movement was recorded within Patch Betakonona. What about these patches promotes movement? Alternatively, is there something about the substrates in patch Betakonona that hinder movement? The few exceptions of moving behaviors recorded for sifaka in Betakonona are only from when the sifaka left the patch and were therefore right on the boundary of the defined area, while no moving behavior was recorded for sifaka actually inside of the patch. Seven sifaka moving occurrences were recorded in Patch 800-900. Out of these seven occurrences, the sifaka were observed to move primarily by two-meter leaps (57.1%) on medium, vertical substrates in quadrant seven at a height as low as one meter up to six to eight meters. Brown lemurs were also noted to not engage in much movement while in Patch Betakonona. As mentioned in chapter three, Patch Betakonona felt colder than the other patches due to consistent low cloud cover and wind. Perhaps this colder environment inhibits movement. During the colder months (August-September) in BNR, the radio-collared lemurs often woke later in the morning and spent more time huddled on a branch or in close proximity to another group member. Temperature may be another factor driving behavior

while in the patch or even the overall use of the patch. This supports the premise that lemur habitat use can be multi-faceted with a broad range of factors influencing their occurrence. As with the brown lemur analysis, the fact that sifaka did not use all patches equally, with some patches more frequented than others, could also have influenced the research results.

Two of the sifaka observed several times in Patch 800-900 were recording marking trees as they moved through heading towards the west. The sifaka moved and marked the trees in the western portion of the patch and would cross over the main trail at 1000 meters continuing their travel to the west outside the boundary of the patch. The sifaka leapt distances from one to four meters in quadrant seven on vertical substrates at variable heights ranging from one to eight meters. In Patch Sahakoho there were only two moving occurrences recorded. On both occurrences the sifaka leapt two meters onto medium, vertical substrates at a height of four to five meters in quadrant seven.

Within-Substrate and Between-Substrate Movement

Another interesting topic for the expansion of understanding different movement patterns within the patch includes an analysis of locomotion posture and the vegetative quadrants used for within-substrate movement versus between-substrate movement. The sample sizes for sifaka movement within Patch 800-900 and around Patch Betakonona are both small (N=7). In both locations the movement was focused on between-substrate movement (85.7%). The one within-substrate locomotor position recorded was a "vertical-bound" for both patches. Vertical clingers and leapers often take an extra hop after landing on the new substrate, or prior to movement the lemur may hop up or down the vertical support in order to achieve a better line of sight or position on the targeted substrate. Between-substrate movement consisted of leaping variable distances in both patches with the sifaka using two meter leaps more frequently (N=4) than sifaka in 800-900, which moved by one and three meter leaps (N=4).

Summary for Sifaka

The surprising discovery was that sifaka inhabit Patch 800-900. This is interesting in that sifaka are the rarest lemur in Betampona, and their survival in the future is of great concern. Upon initial analysis one may suggest that sifaka rarity is attributed to the inherent variables of a habitat specialist such as requiring certain foods and/or habitat type. Sifaka are also large-bodied lemurs that can maintain large territories (Powzyk, 1997). These are all traits that are often attributed to species that experience rapid local extirpation in forest fragments. An important result of this research is that the sifaka in BNR are quite flexible in terms of the number and variety of different patches they utilize, suggesting that heterogeneity of the environment is beneficial to the sifaka.

The patches that the sifaka were never observed to use during the point counts were Sahabefoza, Zubenubi, and Guava. Guava and Zubenubi were both patches that contain abundant low-lying vegetation and liana tangles, the Guava more so than Zubenubi because of the high abundance of guava thickets. This congestion might blur the vertical space for a vertical clinger and leaper, influencing patch choice. However, *Indri* was observed to move through Patch Zubenubi with no hesitation or difficulty. Patch Sahabefoza was a distinctive patch given its close proximity to expansive fields of longoza. Perhaps this longoza created a landscape level boundary for the sifaka or maybe there was nothing in this patch of value to warrant negotiating the longoza. This could also be the case with the guava patch. Sifaka were never encountered south of patch 800-900. Perhaps this transitionary space also creates a boundary.

Another reason could be that sifaka are just too rare to inhabit all of the patches. With a population size of around 22 individuals, perhaps there is still enough "choice" forest to move, eat, and rest. Furthermore, sifaka are territorial lemurs and do actively defend their territory by chasing and threatening other sifaka groups within their boundary (personal observation). Perhaps another important variable in patch use is the social component where lemurs do not use certain patches because of the extent of the home range of another lemur group.

Indri indri

Indri utilized three out of the eight quantified patches in BNR and two were used more frequently than the third. These more frequented patches were Betakonona (37%) and Zubenubi (47%). The least amount of time was spent in Patch Sahakoho (16%) (Figure 5.7). There were also differences in the percentage of time dedicated to the different observed behaviors recorded via the point counts within the patches (χ^2=122.3, df=4, p<0.001). Specifically, within the most frequented patches, the primary behavior was rest, although time dedicated to moving and resting was variable. In Patches Betakonona and Zubenubi, a higher percentage of time was dedicated to eating rather than moving. In Patch Sahakoho the reverse was true where more time was spent moving than eating (Figure 5.8, Table 5.3).

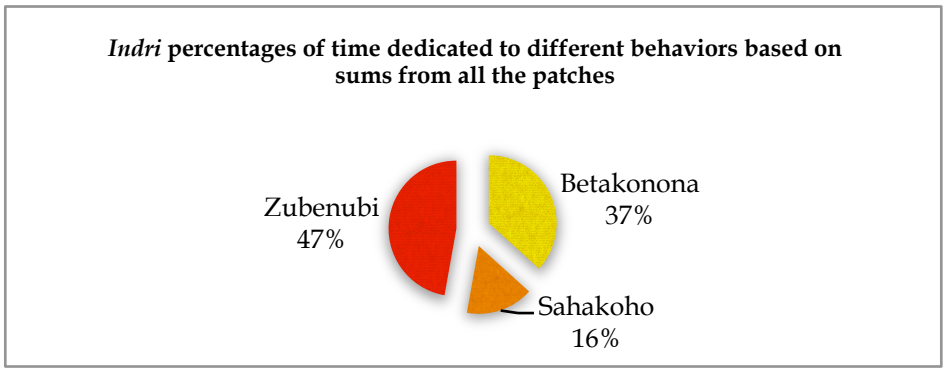


Figure 5.7 *Indri* groups total percentage of time engaged in all behaviors in each patch

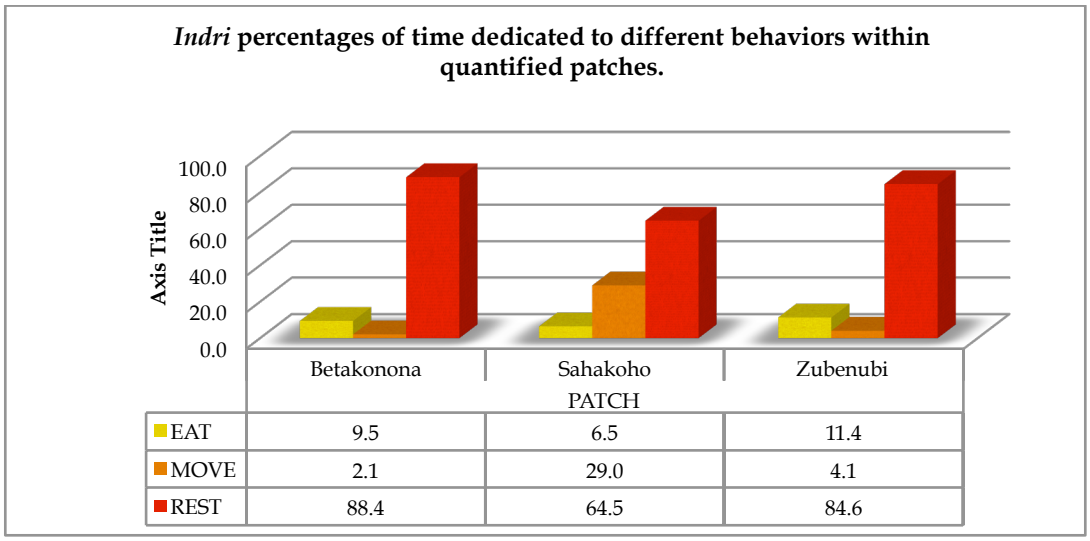


Figure 5.8 Indri percentages of time dedicated to different behaviors within quantified patches

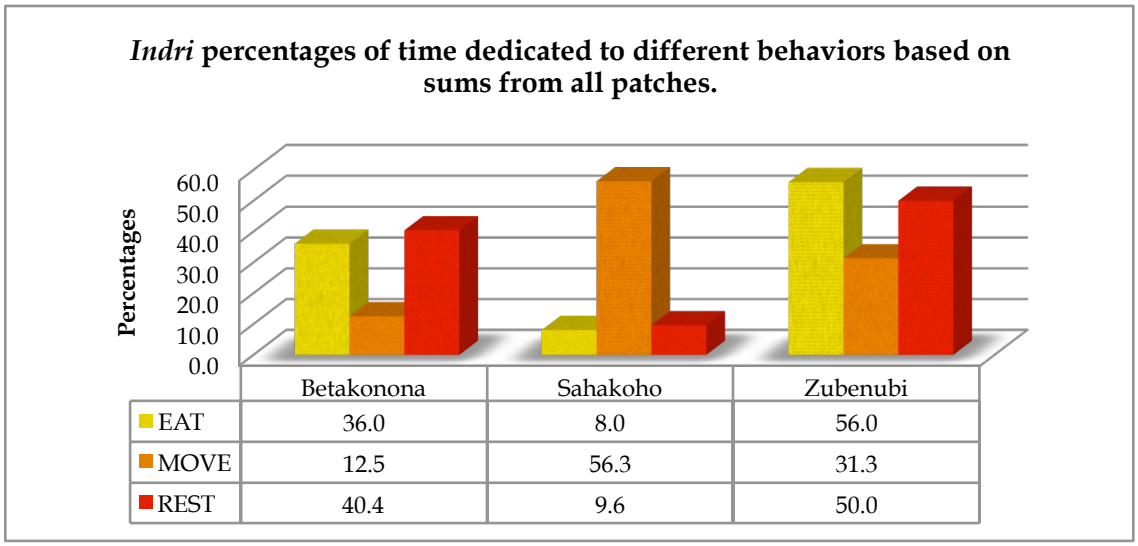


Figure 5.9 *Indri* percentages of time dedicated to different behaviors within quantified patches

Table 5.3 Indri counts of different behaviors within quantified patches

	PATCH		
BEHAVIOR	Betakonona (N)	Sahakoho (N)	Zubenubi (N)
EAT	9	2	14
MOVE	2	9	5
REST	84	20	104

In a comparison based on percentages calculated from the total sum of *Indri* behaviors from all the patches (Figure 5.9), *Indri* rested the most in patches Zubenubi and Betakonona (Figure 5.9). The indri observed in Patch Zubenubi showed a slightly higher percentage of time resting. This higher percentage is due to one individual indri that rested for a prolonged period, perhaps due to fright, after being chased by another indri into this patch. *Indri* moved the most in Patch Sahakoho (56.3%) and the least in Patch Betakonona (12.5%). Furthermore, *Indri* spent the most time eating in Patch Zubenubi, followed by Betakonona, and the least in Sahakoho.

Why are *Indri* resting in Patch Betakonona?

Why were indri resting the most in Patch Betakonona and the least in Patch Sahakoho? An analysis of posture and substrate use reveals that in Patch Betakonona indri spent most of their time resting (85.7%). While resting, indri spent equal proportions of time in either sit-extend

(47.6%) or sit (51.2%) postures on medium, horizontal branches at a height of 7-8 meters (50%), 11 meters (19.0%), or 12-13 meters (28.6%). *Indri* primarily used quadrants four (29.8%) and six (69.0%) for resting. While resting in Patch Sahakoho (N=20), indri used sit (80%), suspensory (5.0%), and vertical clinging (15.0%) postures at the heights of seven to eight meters (65.0%) and nine to ten meters (35.0%), mainly in quadrants six (30%) and seven (65%). *Indri* used horizontal (30%), oblique (50%), and vertical (20%) substrates that were either small (65%) or medium (35%) in size. While resting within Patch Zubenubi (87.5%) indri would vertically cling to small (25.6%), medium (61.1%), and large (12.2%) oblique (80%) or vertical (20%) substrates. Resting in the vertical-cling posture occurred in quadrant seven at various heights including at one meter (6.7%), two to three meters (75.6%), four to five meters (13.3%), and six or twelve to thirteen meters (2.2%). While resting (11.5%) in the adjacent trees to Patch Zubenubi, indri sat on medium, oblique branches in quadrant six at a height of four to five meters (33.3%) or twelve to thirteen meters (66.7%). Within Patch Zubenubi the resting posture of indri was a vertical cling on oblique or vertical substrates. This type of posture was primarily seen in indri when resting between leaping bouts. The indri resting in Zubenubi were often en route to another part of the forest and therefore rest did not appear to be the primary objective of occupancy. Rest in Betakonona, however, appeared to be intentional and on occasion the indri used trees in Betakonona as their overnight sleeping trees. Here, the indri used medium sized horizontal substrates at taller heights, which was a common behavior for indri engaging in extended rest periods. Similar to the sifaka, *Indri* in BNR expressed much variability in their choice of substrates for resting and did not appear to have a heightened preference for particular vegetative attributes. This is in contrast to what was observed for *Eulemur*.

What Patches promote movement for the *Indri*?

Indri moved the most in Patch Sahakoho, to a lesser extent in Patch Zubenubi, and the least in Patch Betakonona. What about these patches promotes movement? Alternatively, is there something about the substrates in patch Betakonona that hinder movement? In Sahakoho, indri exhibited much variability in their use of different substrates and heights for movement. Here leaping consisted of one to three meter vertical leaps on vertical substrates in quadrant seven. *Indri* individuals moved at variable heights ranging from one to ten meters on small (44.4%), medium (44.4%), and large substrates. In Patch Zubenubi, *Indri* approached from the northwest and moved right through continuing on to the eastern portion of the reserve. The sample size for indri moving through this patch was small (N=5). Given how fast the indri moved and the reluctance to linger in this patch, the indri were soon gone beyond the patch boundary before much behavioral data could be collected. *Indri* moved by leaping one to four meters on vertical substrates in quadrant seven that ranged in size from small to large. The height of their movement also varied, ranging from one to three meters. The lianas in this patch form tangles at all levels and angles, creating essentially one closed prominent canopy layer starting from the ground and extending up to seven/eight meters, masking much of the vertical space. On average, 110 lianas were counted per 100 m^2, although in some areas the number of lianas was as high as 158/100 m^2. Despite this cluttered vertical space, indri had little difficulty negotiating their way through the narrow open spaces using tree trunks and lianas along the way, no matter how small the diameter of the substrate or the height.

In Patch Betakonona, indri had only two moving occurrences. One bout consisted of a three meter leap onto a large, vertical substrate at height of eight meters. The other bout was a climb at a height of ten meters on a medium vertical substrate. Patch Betakonona offers a variety of substrates with which the indri could use to move. The use of substrates of varying sizes and heights in Patch Zubenubi illustrates that indri have flexibility in their ability to use a broad range

of structures for movement. Why they do not move as much in Betakonona could be similar to the reasons proposed for the other lemurs observed here that follow this same trend. It could be the colder temperature, the indri's focus on other behaviors while using this patch such as resting or eating, or sample size.

Within-Patch and Between-Patch Movement for *Indri*

Another interesting topic for understanding different movement patterns within the patch includes an analysis of locomotion posture and the vegetative quadrants used for within-substrate movement versus between-substrate movement. Between the three patches that indri individuals were observed to use, only one occurrence of within-substrate movement occurred. This within-substrate movement involved climbing in quadrant seven in Patch Betakonona. The other movement in Patch Betakonona was a between-substrate leap of three meters onto quadrant seven. In Patches Sahakoho and Zubenubi, no within-substrate movement was observed. Between-substrate movement consisted of leaps between one and four meters in quadrant seven on vertical supports. Perhaps there was less within-substrate movement here because of feeding behavior. In Patch Sahakoho, indri spent a small amount of time foraging and so there was no need to move around within the trees. In Patch Zubenubi there was more foraging among the indri, but no accompanying increase in within-substrate movement.

Why do *Indri* devote a higher percentage of time to feeding in some patches over others?

Indri engaged in feeding behaviors the most in Patches Zubenubi and Betakonona, whereas the least amount of feeding behavior was observed in Patch Sahakoho. Why is this? Is it the substrates? Is it food availability? The sample size for feeding behavior was low for all three of these patches. Also, a majority of the trees the indri were eating from could not be identified. Unfortunately then, not much can be said about the species of tree the indri were eating from in relation to food availability in the patch. It can only be noted that the *Indri* was eating young leaves in Patch Betakonona (N=9), mature leaves in Sahakoho (N=2), and mature (N=3) and young (N=11)

leaves in Patch Zubenubi. In Sahakoho, indri were primarily moving through or resting while in this patch with very little feeding behavior. In Zubenubi all of the feeding behavior occurred in the taller trees on the periphery of this patch and the adjacent area. This adjacent area has an overall increase in canopy height as well as an increased number of larger dbh trees. This area also has an increase in plant composition diversity. While eating young leaves indri assumed a sit-extend posture on medium, oblique substrates at a height of nine to ten meters in quadrant five (100%).

Summary for Indri

Indri used three out of the eight patches, suggesting that indri are more limited in the types of patches they use. From a microhabitat standpoint, *Indri* tended to use patches with a taller canopy and clearer understory, although one *Indri* was observed to maneuver through Zubenubi with no problem, making use of the very small substrates and clustered understory. *Indri* also expressed much variability in their substrate use for resting and eating. This suggests that indri were capable of using a variety of substrates if necessary. However, for the indri, the macrohabitat may be more influential in patch choice. The influence of macrohabitat could involve a social boundary component. Even though indri were not observed in every patch, indri were often heard calling from a distance in varying directions from the patch. The duets sung by the indri groups, announcing their territory, could have been a deterrent to some groups not using certain patches. While in Patch Zubenubi I observed what appeared to be one indri being chased by another into this patch. The indri that had been chased remained "stunned" in the patch and the chaser retreated to another part of the forest, indicating there may be vocal as well as active defense of a territory by the indri in BNR, thus promoting or preventing patch use.

Hapalemur griseus griseus

Hapalemur utilized three out of the eight patches (800-900, Sahabefoza, and Fara). Outside of the quantified point counts, bamboo lemurs also used the periphery of the reserve and areas that abut the local village, Rendrirendry (see chapter 3, Patch Guava). *Hapalemur* had the highest

abundances in both patches 800-900 and Fara with the lowest abundance occurring in Patch Sahabefoza (Figure 5.10). There are also differences in the percentage of time dedicated to the different observed behaviors recorded via the point counts within the patches[12]. The biggest difference occurred in Patch Fara where the bamboo lemurs spent a majority of their time resting and no time eating. In Patch Sahabefoza, time was spent moving and resting, also with no time eating. In Patch 800-900, *Hapalemur* spent fairly even amounts of time engaged in all three behaviors (Figure 5.11, Table 5.4).

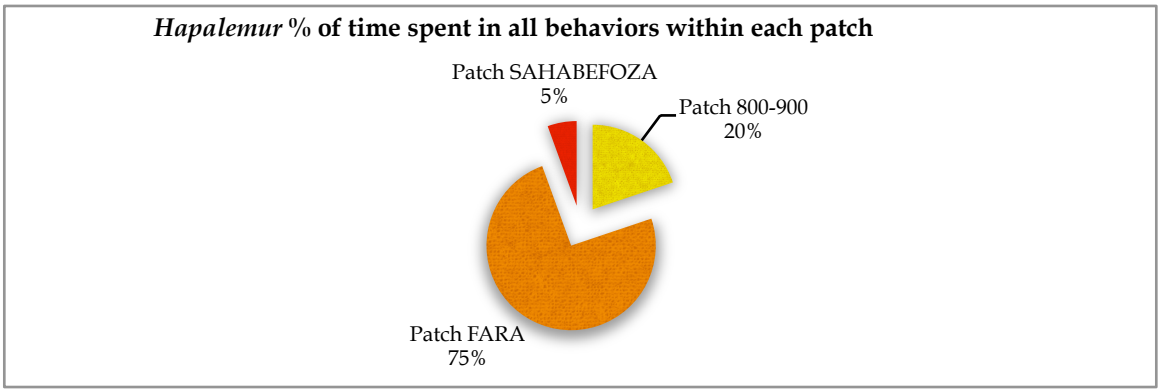
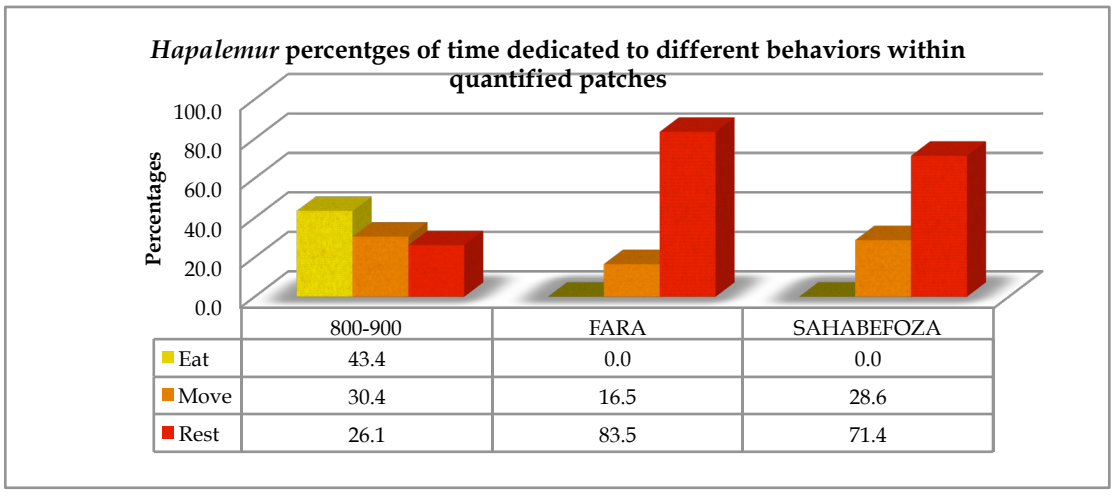


Figure 5.10 *Hapalemur* groups total percentage of time engaged in all behaviors in each patch



	800-900	FARA	SAHABEFOZA
Eat	43.4	0.0	0.0
Move	30.4	16.5	28.6
Rest	26.1	83.5	71.4

Figure 5.11 *Hapalemur* percentages of time dedicated to different behaviors within quantified patches

[12] More than 20% of the expected frequencies were less than 5 therefore a Chi-Square could not be run.

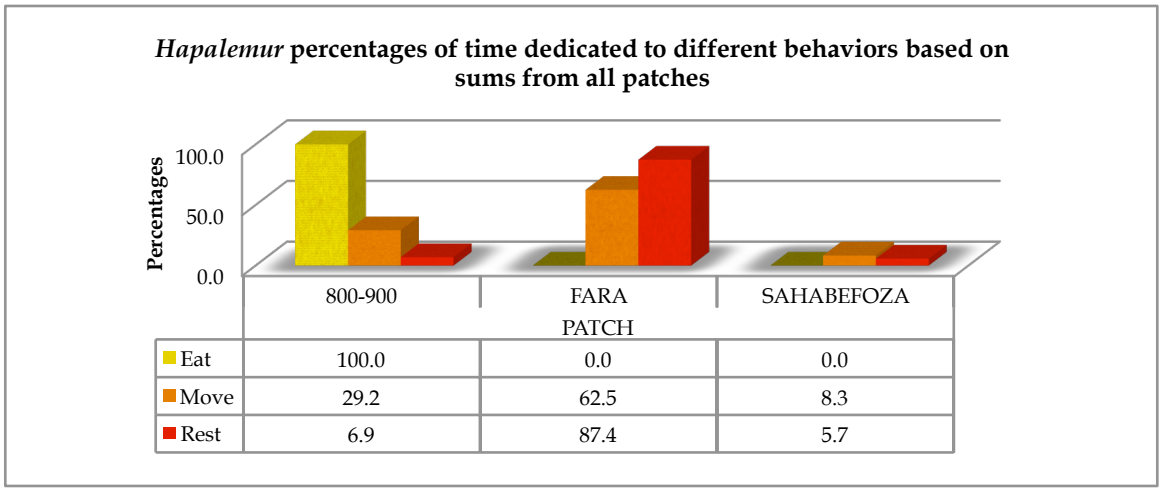


Figure 5.12 *Hapalemur* percentages of time dedicated to different behaviors based on sums from all the patches

Table 5.4 *Hapalemur* counts of different behaviors within quantified patches

	PATCH		
BEHAVIOR	800-900 (N)	FARA (N)	SAHABEFOZA (N)
EAT	10	0	0
MOVE	7	15	2
REST	6	76	5

In a comparison based on percentages calculated from the total sum of *Hapalemur* behaviors from all the patches (Figure 5.12), bamboo lemurs were only observed to engage in feeding behavior while utilizing Patch 800-900, whereas a majority of the resting (87.4%) and moving (62.5%) occurred in Patch Fara. *Hapalemur* engaged in feeding behaviors the most in Patch 800-900, whereas no feeding behavior was observed in Patches Fara and Sahabefoza. Why is this?

Why do Bamboo lemur spend more time feeding in Patch 800-900?

In Patch 800-900 there are several clumps of viney bamboo that the bamboo lemurs frequented and concentrated their feeding time in. *Hapalemur* individuals ate the bamboo leaves while vertical clinging to very small, oblique and vertical substrates one meter in height comprised

of a cluster of bamboo, a tree fall, and a viney liana tangle. The bamboo lemurs were well hidden while feeding on this bamboo. Bamboo lemurs were observed on several occasions occupying this particular bamboo thicket, suggesting it is an important feeding patch for this group of bamboo lemurs. Patch Sahabefoza contained no bamboo, whereas Patch Fara was the only quantified patch to contain stalks of giant bamboo ten meters high with a 7 cm dbh. The bamboo lemurs were not observed to eat and/or use the giant bamboo while in Patch Fara. The giant bamboo was not equally distributed throughout Patch Fara but rather formed a tight cluster of nine stalks. The locations of the pockets of viney bamboo perhaps influenced the utilization of certain patches over others for bamboo lemurs in BNR. Because bamboo lemurs were found in two other patches that lack bamboo there may be other factors influencing their patch choice. Moreover, bamboo lemurs are small, cryptic animals and as such, could very well utilize a patch while going undetected. This could be especially true of bamboo lemurs using the taller canopy. While the bamboo lemurs were more readily detected in the lower canopy, groups in the taller canopy could easily slip away with no detection. When the *Hapalemur* groups knew they had been detected while occupying the lower heights they gave distinctive alarm calls and plunged deeper into the dense layers of the canopy and soon were gone. It is also worth noting that bamboo lemurs using Patch 800-900, a patch closer to the forest edge, were much more vigilant and quicker to give alarm calls than those bamboo lemurs further north. This also holds true for the bamboo lemurs utilizing the viney bamboo on the forest edge and even inside of the village. Perhaps this suggests a response to hunting pressure by the bamboo lemurs inhabiting areas where negative human contact is more frequent, either historically or more recently.

Although no eating behaviors occurred, bamboo lemurs did move and rest while using Fara (Table 5.4). When resting, the bamboo lemurs sat in the tail wrap posture a majority of the time (88.5%) at a height of two to three meters on horizontal and very small lianas. Lianas were the predominate quadrant used out of all the possible quadrants available in Patch Fara. Fara has one

of the lowest abundances of lianas in comparison to the other patches. The bamboo lemurs appeared to choose their travel paths carefully by seeking out these lianas for movement as a means to reach their final destinations of preferred resting sites on select lianas. Despite the available larger sized substrates and taller canopy in Patch Fara, bamboo lemurs still primarily used heights of two to three meters and very small substrates.

Why are the bamboo lemurs moving more in Patch Fara?

The highest abundance of bamboo lemurs occurred in Patch Fara. A higher percentage of moving behaviors were recorded in Patch Fara. *Hapalemur* moved through this area by quadrupedal locomotion (46.7%) and by leaping less than one meter (20%) and one meter (33.3%), making use of very small (60%), small (26.7%), and medium (13.3%) substrates. When moving the bamboo lemurs used oblique (53.3%) and vertical (33.3%) substrates at a range of heights varying from one meter to ten meters.

Hapalemur also equally used a variety of different quadrants, including four, five, six, seven, the longoza stems, and lianas. Several groups of *Hapalemur* were observed moving through Patch Sahabefoza. Yet, the sample size was small, consisting of seven individuals. *Hapalemur* in contrast to *Eulemur*, moved right through the longoza field vertical-clinging-and-leaping from one vertical support to the next. The group moved in a single line one waiting for, and following the next in line. *Hapalemur* individuals moved through the patch near plot 4 towards the smaller 25 m^2 patch of longoza between the forested areas. The bamboo lemurs also moved through a 100 m^2 longoza patch. The longoza stems used to move and periodically rest were small dbh, vertical substrates two meters in height. The bamboo lemurs also used small horizontal and vertical lianas to move and rest at a height of one meter. In Patch 800-900, *Hapalemur* moved by leaping one to three meters on small and medium, vertical substrates at a height of two to five meters. When resting, the bamboo lemurs would cling to very small, and in some cases medium, oblique and vertical substrates. Resting occurred at a height ranging from one to three meters in quadrant seven or

within the liana tangles. In Patch 800-900 rest was usually in between locomotor bouts and not a prolonged relaxed behavior. Bamboo lemurs used multiple sized substrates and heights for movement. This flexibility suggests their ability to use all of these patches equally for movement.

Within-Substrate and Between-Substrate Movement

Bamboo lemurs focused more on between-substrate movement than within-substrate movement for Patches 800-900 and Sahabefoza. Patch Fara shows a fairly equal amount of time spent in both kinds of movement by the bamboo lemurs. In Patch Sahabefoza the bamboo lemurs only engaged in between-substrate movement using liana and longoza stems. The sample size was small (N=2) for movement within the patch but the bamboo lemurs were observed to use between-substrate movement through the longoza to get to the patch on the other side of the field. Bamboo lemurs used one meter leaps for this between-substrate movement. In Patch 800-900 bamboo lemurs primarily used between-substrate movement with just one instance of within-substrate movement that entailed bounding down a ravinala trunk. The between-substrate movement consisted of one (N=4) and two to three (N=2) meter leaps mainly onto quadrant seven (N=4) or through liana tangles (N=2). In Patch Fara the bamboo lemurs used small leaps (≤1 m) (N=8) for between-substrate movement in quadrants seven, the longoza, and lianas. The bamboo lemurs used quadrupedal locomotion (N=7) for within-substrate movement, using quadrants four through six.

The bamboo lemurs exhibited an ability to use a variety of substrates and quadrants for between-substrate movement suggesting they were not inhibited and perceived a high degree of connectivity throughout the forest. The total number of bamboo lemurs living in BNR is relatively high in comparison to the other lemur taxa and based on data recorded from this research, bamboo lemurs appeared to be quite flexible in their behavior and movement patterns. Why bamboo lemurs were not encountered more often is interesting and could again be attributed to the fact that these lemurs are small, quiet, and can move quickly.

Summary for Bamboo lemurs

In sum, the bamboo lemurs used a variety of different patch types. The fact that they were only observed in three of the eight patches may be due to the cryptic nature of bamboo lemurs and their potential ability to quietly use taller heights with no detection and not necessarily their inability to use the other five patches. The three patches that the bamboo lemurs were recorded in are very different and suggest flexibility in the behavior of bamboo lemurs. Patch Fara is primary rainforest boasting the tallest canopy of all the quantified patches. Although considered primary rainforest, there is a small patch (25 m^2) of longoza that has taken advantage of a light gap in the northern section of the patch. The bamboo lemurs frequented this portion of the patch even using the longoza stems for movement and nearby lianas. Even though there are large substrates and taller canopy available for use in this patch, the bamboo lemurs still used small substrates at lower heights.

Patch 800-900 is located in the transition area of the reserve and shows an eclectic range of different substrates and plant composition. There is a keystone bamboo bush in this patch that bamboo lemurs frequented suggesting this is an important structure to these lemurs. An important result of this research was the observation of bamboo lemurs readily utilizing longoza stems as viable substrates for movement. Patch Sahabefoza is bordered by fields of longoza to the south and west and a river valley to the north. The bamboo lemurs moved by vertical-clinging-and-leaping from stem to stem across 400 m^2 fields to the forest patch on the opposite side. This adjacent patch of forest contained 50% viney bamboo clustering around several tree falls and liana tangles. Bamboo lemurs were observed to eat this bamboo. In contrast, the brown lemurs in Patch Sahabefoza never crossed through the longoza but instead used the sporadic perimeter trees, and even in sections, the ground to make their way around the longoza fields to adjacent areas of forest. Bamboo lemurs also exhibited their flexibility and ability to cope with anthropogenic change in BNR by their use of bamboo growing on the perimeter of the reserve and near houses frequented

by people inside of the village. The bamboo lemurs that did use these areas were hyper-vigilant and quick to give an alarm call and flee when detected.

Varecia variegata

Varecia was observed to only use Patch Fara. Although *Varecia* was often heard calling some distance away, they were rarely seen during point counts or among opportunistic sightings in the forest. The only other patch that *Varecia* were observed, albeit from a distance, was the area adjacent to Sahabefoza. Three *Varecia* were observed and also heard giving their roar/shriek chorus from a distance but never in the plot. To the west and abutting the longoza field are several 25 meter tall partially dead trees that the ruffed lemurs were calling from. After the vocal consternation, the group continued off to the west. *Varecia* were never observed moving through or using this patch.

While in patch Fara the ruffed lemurs were not observed to engage in any feeding behaviors. *Varecia* moved mainly by quadrupedal locomotion (83.3%) with the occasional two meter leap (16.7%) on medium horizontal (58.3%) or oblique (41.7%) substrates. When moving, the ruffed lemurs primarily used quadrant three at heights ranging from ten to fifteen meters. If their movement patterns are divided into the two categories of within-substrate and between-substrate movement, the ruffed lemurs spent more time engaged in within-substrate rather than between-substrate movement. This is interesting in that this is the opposite pattern observed among all the other lemur groups when conducting a comparison between these two types of movement. The sample size is small and so it is difficult to make any major conclusions. Plus, the ruffed lemurs were not observed in any of the other patches and so a comparison is not possible to be able to suggest that this typical behavior for ruffed lemurs. Ruffed lemurs used quadrupedal locomotion for within-substrate movement, occupying quadrants three (N=5), five (N=3), and six (N=1). There was a sample size of three for between-substrate movement consisting mainly of two meter leaps and one occurrence of quadrupedal locomotion by moving through the connected

canopy in quadrant five. The lemurs were not foraging for food in this patch and a reason for the within-substrate movement may have been more about finding a comfortable resting spot.

The ruffed lemurs were observed to rest in Patch Fara. The ruffed lemurs rested primarily in a recline posture (91.1%) on medium and large horizontal (70.7%) and oblique (29.3%) substrates. The ruffed lemurs rested at a height of nine to ten meters (33.3%) or fourteen to fifteen meters (64.4%) in quadrants three (26.7%), four (37.8%), and five (26.7%).

The ruffed lemurs mainly took advantage of the taller canopy in Patch Fara and used trees ≥ 15 meters in height. Ruffed lemurs are rare in BNR with an estimate population size to be around 35 individuals. The dwindling number of ruffed lemurs in BNR caused such concern that in the 1990s this population was targeted with a restocking program in order to increase the population size and genetic diversity. Out of the original ruffed lemurs introduced, only one male, Snarf, remains. He has successfully mated with wild ruffed lemur females, producing viable offspring and introducing new genes into the population. The fate of the ruffed lemur population in BNR is still of the utmost concern. The fact that they were only observed in one patch was disheartening but not that surprising. Ruffed lemurs are frugivorous, requiring primary rainforest with keystone fruit trees. Ruffed lemurs have been recorded repeatedly to be one of the first species to experience local extirpation once the vital fruit trees have been removed (Britt et al., 2003a). Ruffed lemurs were not observed to eat foods in Patch Fara, which may be a result of the seasonal availability of food sources at the time of this research.

Avahi laniger

A group of three *Avahi*, including a female with a very young infant still riding ventrally, was observed to utilize only one patch, Patch Betakonona, during the point count sessions. In addition, *Avahi* on two separate occasions was caught via the camera trap in Patch Sahakoho. One of these photos was taken at night evidenced by the complete darkness and the other taken at some point

during the day or late afternoon. The photo taken during the day captured an individual carrying a very young baby still riding ventrally.

The extended observation of this nocturnal lemur between the hours of 11:00 AM and 3:00 PM was an important result and unexpected. These individuals were rather active and ate mampay leaves 22% out of their total time whereas 66.9% of their total time was spent resting. While resting the *Avahi* sat (98.8%) on medium, oblique substrates, at a height of six meters in quadrant six (91.7%) or within the liana tangles (8.3%) ensconcing the tree. The *Avahi* were active off and on in terms of grooming and eating from when they initially leapt into this patch up until the point they left heading further west. The only movement briefly recorded for the *Avahi* was when they entered the patch and when they left. This movement consisted of one meter leaps onto small substrates in quadrant seven at a height of four meters.

This was an interesting observation because *Avahi* are nocturnal primates and so observing them during the day actively eating and grooming was unexpected. In Patch Sahakoho *Avahi* were also observed to be active during the day via the camera traps. BNR contains six nocturnal lemur taxa that are largely understudied and will be an important area of focus in the future for their own intrinsic value but also how spatial pattern and heterogeneity influence their distribution in a forest fragment.

Summary: Does scale affect community structure and behavior?

MICROHABITAT

Microhabitat affects lemur community structure, although the degree to which each lemur taxon is affected varies. Brown lemurs were found in all eight patches but frequented some patches more than others. Furthermore, the brown lemurs engaged in different behaviors at a higher frequency in some patches with this variation perhaps attributed to microhabitat structures. For example, brown lemurs rested more so in Patch 800-900. This could be attributed to the abundant 1-5 cm dbh trees, lianas, and dead standing/fallen trees that clutter much of the horizontal and

vertical space. The overall canopy height here is also relatively low. Additionally, Patch 800-900 contained favored ramy trees that are ensconced in lianas, providing a protective refuge for the brown lemurs. Brown lemurs regularly slept in these trees during the day but also used them as overnight sleeping trees. The brown lemurs showed a heightened preference for feeding in Patch Zubenubi. Lianas had the highest average abundance per 100 m^2 in Patch Zubenubi perhaps attracting the brown lemurs to this location as the brown lemurs often fed on the liana fruits. The brown lemurs also ate the fruits of the abundant hazomainty trees and palms found in this patch. At first glance, Zubenubi appeared to be an insignificant degraded area, but upon further investigation, this is an important foraging area for the brown lemurs.

Indri used three out of the eight patches, suggesting that indri were more limited in the types of patches they used. From a microhabitat standpoint, *Indri* individuals tended to use patches with a taller canopy and clearer understory, although one *Indri* was observed to maneuver through Zubenubi with no problem, making use of the very small substrates and clustered understory. *Indri* also expressed much variability in the substrate used for resting and eating. This suggests that indri are capable of using a variety of substrates with no particular preference and implies that microhabitat does not have much of an effect on their patch choice (Although this is explored further in chapter 7 in light of a comparison made with the radio-collared indri groups). The observation that indri occurred only in three of the patches suggests that the macrohabitat may be more influential than microhabitat in patch choice.

Microhabitat may influence bamboo lemur occurrence. For example, in Patch 800-900 there were several clumps of viney bamboo that the bamboo lemurs frequented and where they concentrated their feeding time. The bamboo lemurs were observed on several occasions to occupy this particular bamboo pocket, suggesting this is an important keystone vegetative attribute to the bamboo lemurs. In patch Sahabefoza, the bamboo lemurs were observed to move 20 meters through a patch of longoza to reach the forest on the other side. This adjacent forest patch contains

ample viney bamboo that the bamboo lemurs consumed. The bamboo lemurs were observed to engage in this behavior on several occasions suggesting that these bamboo pockets are important forest attributes to the bamboo lemurs of BNR. In Patch Fara, the microhabitat features that appeared important to the bamboo lemurs were the lianas. Lianas have a low density in Patch Fara. Despite this, and the availability of a broad range of substrates to choose from, the bamboo lemurs chose their travel paths carefully by seeking out these lianas for movement as a means to reach their final destinations of preferred resting sites on select lianas. Despite the available larger sized substrates and taller canopy in Patch Fara, bamboo lemurs still mainly used heights of two and three meters on very small substrates.

As noted above, an important result of this research was that the sifaka in BNR are quite flexible in terms of the number and variety of different patches they utilize. The sifaka were observed in five of the eight patches, the second highest patch distribution. While in a patch, sifaka made use of a variety of microhabitat attributes. Repetitive use of favored specific trees or their attributes was not observed other than the preference for quadrant six (i.e. lowest part of the canopy closest to the trunk) on small substrates. This vegetative attribute is common and is not patch specific. The variety of microhabitat features used by the sifaka allows them to exploit any of the patches, leaving them unhindered by the restrictions of specific vegetative attributes.

Varecia groups were only observed in one patch, Fara, and seemed to be the most affected by microhabitat in comparison to all of the other diurnal lemurs. Fara contains the tallest canopy in comparison to all of the other patches. The ruffed lemurs were observed to only use this taller canopy for resting and moving. The ruffed lemurs were not observed to consume any foods while in Patch Fara, so the importance or significance of certain feeding trees remains unknown.

MACROHABITAT AND LANDSCAPE

Macrohabitat and landscape scales affect lemur community structure, although certain features appear to have more of an affect than other features. For example, the topography

(location on ridges versus valleys) of the patch did not seem to affect the different lemurs' patch choice. Moreover, similar to the microhabitat features, the degree to which each lemur taxon was affected by macrohabitat varied. For example, Patch 800-900 appeared to be a boundary below which three of the five diurnal lemurs were not observed to move. The guava is not a boundary for the brown lemurs or bamboo lemurs, taxa that still perceive connectivity through this forest characteristic. As such, these lemurs were not limited in their dispersal or use of different patches throughout the entire reserve. *Eulemur* and *Hapalemur* also used patches (e.g. Sahabefoza) that were adjacent to large expanses of longoza fields even though this macrohabitat feature contributed to a lack of connectivity across the landscape. The other diurnal lemurs were not observed to use or move through this patch perhaps due to the perceived boundary of the longoza.

An important discovery of this research was that sifaka were observed to use five of the eight patches. This is interesting because sifaka are the rarest lemur in Betampona and their continued survival is of extreme importance. Understanding why the sifaka population is so low is necessary for the implementation of an action plan to increase their numbers in BNR. Conceivably, this rarity could be due to the inability to use certain areas of the reserve thus limiting dispersal and access to different resources. However, the sifaka appeared to be quite flexible in terms of the number and variety of different patches they utilized. The population of sifaka in BNR has always been small, low numbers were reported even with some of the first surveys conducted in the early 1990s. The fact that the sifaka population has not gone locally extinct is remarkable and may be attributed to their behavioral plasticity and use of the full range of heterogeneity within BNR.

The patches that the sifaka were never observed to use during the point counts were Sahabefoza, Zubenubi, and Guava. The Guava and Zubenubi were both patches that contained abundant low-lying vegetation and liana tangles, the Guava more so than Zubenubi because of the high abundance of guava thickets. This congestion may blur the vertical space for a vertical-clinger-and-leaper, influencing patch choice. Patch Sahabefoza was a distinctive patch given its close

proximity to expansive fields of longoza. This longoza created a landscape level boundary for the sifaka or maybe there was nothing in this patch of value to warrant negotiating the longoza. This scenario could also be the case with the guava patch. Sifaka, indri, and ruffed lemur groups were never encountered south of patch 800-900. Perhaps this transitionary space also created a boundary.

Another macrohabitat component could be a social component. Even though the indri individuals were not observed in every patch, indri were often heard calling from a distance in varying directions from the patch. The duets sung by the indri groups, announcing their territory, could have been a deterrent to some groups not using certain patches. While in Patch Zubenubi I did observe what appeared to be one indri being chased by another into this patch. The indri that had been chased remained "stunned" in the patch and the chaser retreated to another part of the forest, indicating there may be vocal as well as active defense of a territory by the indri in BNR, thus promoting or preventing patch use.

Hapalemur used three out of the eight quantified patches. Although the bamboo lemurs were just observed in three patches during the point counts, they were also observed to use the area around the perimeter of the reserve. This perimeter use included feeding on bamboo thickets growing in close proximity to village houses. Although these lemurs were only observed in several patches, the patches the bamboo lemurs used were quite different from one another. This may indicate behavioral flexibility in their use of a heterogeneous landscape. Furthermore, the fact that bamboo lemurs were observed in only three patches and not all eight may be due to their cryptic nature and small size. Perhaps the lemurs used the patch and left, going undetected.

The bamboo lemurs moved directly through the longoza field growing adjacent to Patch Sahabefoza to reach the forest patch on the other side. This ability to move through this macrohabitat/landscape feature of a potential perceived boundary suggests that bamboo lemurs were not limited by connectivity inside of the reserve. The bamboo lemurs further expressed their

flexibility to anthropogenic change by regular use of both the perimeter of the reserve and the bamboo growing inside of the village Rendrirendry in close proximity to human activity.

Local habitat quality may be assessed by an organism in part as a function of what habitat quality is adjacent to a given habitat patch (Figure 5.13) (e.g. Lindenmayer et al., 1999; Steffan-Dewenter et al., 2002). It is not only important to quantify *what* a patch is but also *where* it is in terms of neighboring ecological properties that filter certain organisms. Prominent examples of this in BNR include the longoza fields adjacent to Sahabefoza and the transition zone of Patch 800-900 adjacent to the guava. The longoza patch may impede certain lemurs from using the surrounding areas due to the quality of the adjacent patch that is perceived as poor by the lemurs. The only two lemurs observed in Patch Sahabefoza were brown lemurs and bamboo lemurs. The brown lemurs were able to use the adjacent trees, the ground, and low vine tangles to move around the field whereas the bamboo lemurs moved directly through the longoza using this vegetation as a viable moving substrate. This was an important observation of this research, providing an enhanced understanding of how different lemur taxa perceive connectivity.

Brown lemurs and bamboo lemurs were also the only lemurs observed in the guava and inside of the nearby village, Rendrirendy. Perhaps the adjacent patch of 800-900 is deemed a poor quality patch and so some lemur species proceed no further. The guava produces abundant fruit during certain times of the year; fruit that one might expect to attract frugivores such as the ruffed lemur. However, ruffed lemurs have never been observed in the guava. Perhaps this is due to the perceived quality of the adjacent patch, 800-900, which prevents the ruffed lemurs from continuing any further. Alternatively, the lack of use may be due to the microhabitat attributes of the guava itself that consists of a low canopy and congested understory or some intricate combination of these different spatial levels.

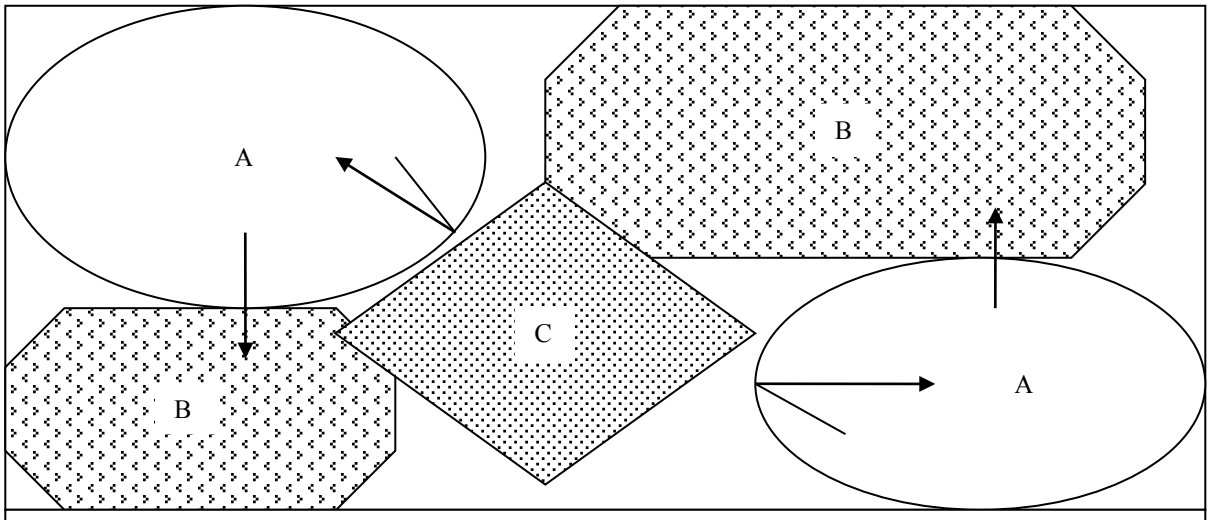


Figure 5.13 Patch context is the structural configuration of the mosaic in which the patches are embedded (Wiens, 2002). The boundaries of the patches act as 'membranes' that filter the flow of organisms in and out of the patch. For example, the figure above illustrates a heterogeneous landscape emphasizing patch context. Individuals can move (arrows) from patch A to B if the boundaries are considered permeable but are unable to move to C due to unsuitable habitat to cross in between the two patches.

In conclusion, it would be ideal to identify single features that influence an entire community of lemurs where removing this variable would result in complete ecosystem collapse. However, this research demonstrates that it is inappropriate to reduce the complexity of the rainforest into a single variable and that this variable is not the same for all lemurs. This is an important outcome of this research and what allows these five diurnal species to continue to co-exist in a forest fragment. Spatial pattern does seem to impact the occurrence of lemur taxa throughout BNR with some lemurs incorporating more environmental heterogeneity into their activity pattern like brown lemurs, sifaka, and bamboo lemurs, whereas for others, such as ruffed lemurs, this heterogeneity is more detrimental.

Quantifying the variation in lemur habitat use across the landscape and identifying habitat structural variables and patterns at a micro – and macrohabitat level is an important component in understanding the primate community assemblages in different habitat types throughout BNR. A

map is presented below illustrating the distribution of the diurnal lemur taxa within the different patches of BNR (Figure 5.14).

The point counts only provided a limited assessment of the behaviors displayed by the community of lemurs in the different patches. Behavioral data were collected on the lemurs while in the patch, but this use of the patch was such a small component of their day. These limited data may provide a misleading conclusion. The next chapter discusses a more detailed analysis of behavior and vegetation structure from specific lemur groups that were radio-collared and followed to account for their full day of activity in different months. This provided a more robust quantification and focus on a single lemur taxon.

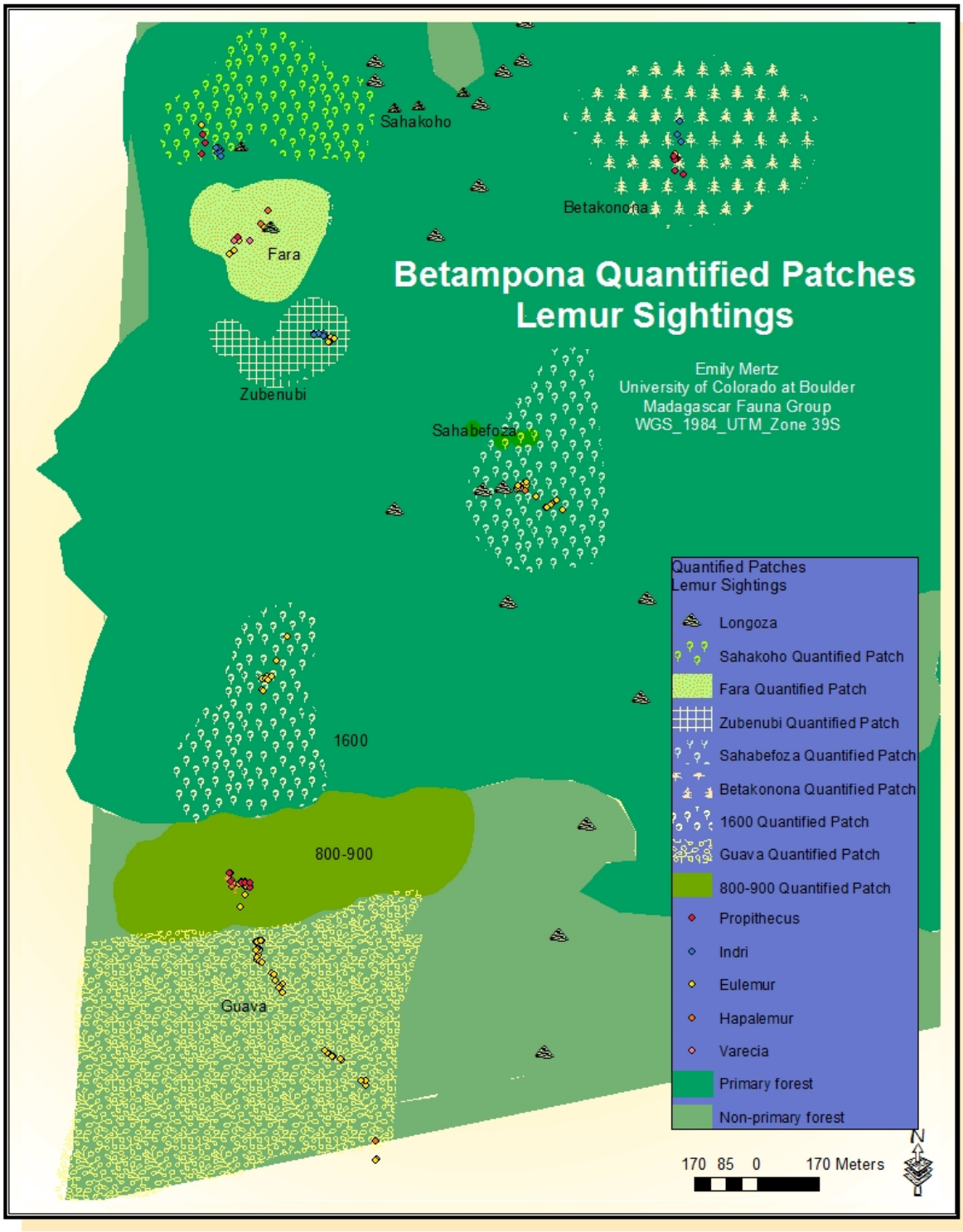


Figure 5.14 GIS map indicating the lemur taxa observed during the point counts

CHAPTER 6
ANALYSIS OF BEHAVIORAL DATA AND VEGETATION STRUCTURE FROM ALL DAY FOLLOWS

Overview of Chapter

The previous chapter presented results on community structure variation in relation to spatial scale in BNR. This analysis was limited in that behavioral data were recorded only for the amount of time the lemurs utilized the patch. As such, large components of their daily activity were not documented. To compensate for this limitation, all-day follows of radio-collared lemurs were conducted in order to account for a more detailed interchange between vegetation structure and behavior. Each group was followed for two consecutive days on a monthly rotational basis.

The main goals of this chapter consist of two components. The first component, labeled Section I: MICROHABITAT, is an analysis of the behavioral and positional use on different substrates by three radio-collared lemur taxa to address questions pertaining to the importance of small-scale attributes to patch choice. Also included in this discussion is the importance of keystone structures (i.e. important feeding, resting, moving structures). Ultimately, this type of information is valuable for reforestation projects including human-made corridor projects. Forest regeneration is a long-term goal for corridor projects to connect forests or even replace patches of forest within the fragment itself. Corridor projects have limitations, including cost, upkeep, and monitoring (e.g. Hilty et al., 2006), but are promoted as a viable conservation strategy (Chetkiewicz et al., 2006; Gilbert-Norton et al., 2010). An interim plan directed towards the capacity to build temporary structures to support the continued survival of lemur communities would be of value. As mentioned in chapter one, this has already begun in Madagascar with the construction of bridges over vast pipelines to maintain a certain level of connectivity. Unfortunately these bridges were more of an afterthought and not custom made based on lemur habitat preferences. As is sometimes the case, a conservation plan is rushed to fit the immediate needs of a crisis. If possible, we need to be more proactive and not wait until disaster strikes. The information collected in this research

will be able to address questions such as the following: what types of habitat features are important for the different lemurs? What types of structures should be built to enhance movement? What lemur taxon is the limiting factor? As part of this first component, the effects of substrate combinations on lemur usage are discussed in detail for each lemur group. Presented within each lemur group analysis are several examples of the substrate combinations that are pertinent to the application of forest restoration.

Some discussion is also given to the nearest neighbor of the focal animal. The proximity of the nearest neighbor may provide insight into intra-group competition based on patch-quality. For example, having constant group cohesion may imply less competition for resources than groups that exhibit more social spacing.

Section I of this chapter is divided into eight subsections, each of which analyzes a different radio-collared lemur group, focusing on the following question and hypotheses. The hypotheses focused on resting and moving because with these behaviors there is a choice by the lemur to preferentially use certain substrates and not others. With feeding behaviors, the lemurs are constrained by the distribution of foods and their growth patterns, perhaps forcing the use of certain substrates and thus limiting the active choice by the lemur. The location of the food may be driving the lemurs to use certain areas and not necessarily the microstructure *per se*. The substrate structure co-varies with the food item eaten, making the microhabitat structure a secondary component and its true affects difficult to isolate without conducting a detailed assessment of all the available substrates in comparison to what is used by the lemur. Feeding ecology was not the focus of this dissertation but lemurs, and primates in general, can spend fifty percent of their day foraging for food, making this behavioral aspect important to address at some level in this analysis. Even though the structure of the substrate the lemurs used for food consumption may be a secondary effect of the distribution of food growth, some interesting patterns emerged in preferentially selecting microhabitat features over others when feeding on particular food items in

the patches utilized by the lemurs. Finally, a comparison of the microhabitat use among the radio-collared lemurs is provided in addition to a recommendation for corridor projects based on the presented results.

The second component of this chapter, labeled Section II: MACROHABITAT, provides a comparison between the lemur groups in the context of the importance of heterogeneity and how patch configuration and composition affect lemur movement patterns and patch use in BNR. Does landscape spatial pattern and heterogeneity influence movement and habitat use for indri, sifaka, and brown lemurs? Some level of control over the environment was accomplished by an in depth analysis of eight quantified vegetation patches within BNR, as presented in Chapter three. The patches were returned to on a regular basis in order to observe the diurnal lemurs utilizing the patch. To assess where the lemurs were going while not in any of these patches, radio-collars were placed on eight lemurs in different groups from three lemur taxa. These different groups were part of all day follows on a rotational basis so that behavioral data could be collected as well as the path of movement and use could be recorded via GPS. GPS points were collected over the course of the all-day follows for each lemur group. Additional plots were established in the areas repeatedly used by the radio-collared lemurs and were quantified following the same methodology as that used for the eight patches. The patches in addition to the plots were also incorporated into a GIS to represent what the lemurs were using in relation to where the lemurs were going. These points, along with their associated attribute data, were analyzed in a GIS and presented as a visual map. This provides a greater understanding of where the lemurs were moving in relation to the different patch types of BNR.

How do local architectural attributes and patch context affect ecological processes such as lemur behavior, movement, and positional behavior?

The following hypotheses were evaluated for each radio-collared lemur group:

H_1: Microhabitat affects resting behavior. If this is the case, then the lemur should be selective in their use of substrates when resting for extended periods.

H_2: Microhabitat affects movement patterns. If this is the case, then the lemur should be selective in their use of substrates when moving through their environment.

H_3: Macrohabitat affects movement patterns. If this is the case, then the lemur should be limited in their patch use and even confined to certain areas.

Section I: MICROHABITAT

Subsection 6.1
SIFAKA GROUP 1

PROPITHECUS GROUP 1: Group composition consisted of one adult male and two adult females. Both adult females in the group gave birth, and one of the infants survived past three months.
Male purple collar (Gus). 6.0 kg, body length 49 cm, tail 49 cm.
Female radio collar (Ruth). 6.0 kg, body length 49 cm, tail 50 cm
Female no collar (Claire). Not captured.

Summary of substrate use and total activity budget for *Propithecus* in Group 1:
Overall size of substrate: A (3.8%), B (51.0%), C (37.3%), D (7.8%), Ground (0.1%)
Overall height of substrate: A (1.7%), B (1.9%), C (8.0%), D (11.8%), E (17.9%), F (26.5%), G (24.2%), Ground (0.1%), H (7.4%), I (0.6%)
Overall quadrant: Quad1 (5.3%), Quad2 (14.5%), Quad3 (6.4%), Quad4 (13.4%), Quad5 (8.9%), Quad6 (30.1%), Quad7 (14.8%), Quad8 (0.1%), 5RavPalm (0.5%), Epiphyte (0.2%), Liana (5.7%)
Overall orientation: A (33.9%), B (49.0%), C (17.0%)
Total activity budget: Eat epiphyte (0.8%), Eat fruit (1.8%), Eat flowers (6.2%), Eat leaves (14.0%), Eat leaf stem (0.3%), Eat seeds (3.9%), Eat young leaves (5.3%), Groom baby (2.4%), Groom other (0.5%), Groom-self (6.5%), Move (10.7%), Mark (0.5%), Tisk (0.2%), Rest 47.0%
Total tree height: B (0.1%), C (0.8%), D (0.9%), E (11.4%), F (30.9%), G (35.9%), Ground (0.1%), H (18.6%), I (1.2%)

The range of *Propithecus* group 1 was in the northern portion of the research area close to Patch Sahakoho. Ruth and Gus both appeared healthy from the initial assessment. Both females gave birth during the course of this field research – Claire in June to Henry and Ruth in September to Thomas. In July, August, and September the group often split with Ruth going her separate way from Gus and Claire a majority of the day. In October and November the group traveled, foraged, and rested together more frequently which allowed observations of both infants. Unfortunately, Claire showed up one day without Henry. It is unknown how or when Henry died. Thomas appeared to be in good health when this research projected ended. The behavioral and movement

data collected from this group was primarily based on observations made of the radio-collared adult female and her nearest neighbor. Out of the overall total activity budget for sifaka group 1, they spent 47% of the time resting, 10.7% moving, and 32.3% eating (Figure 6.1).

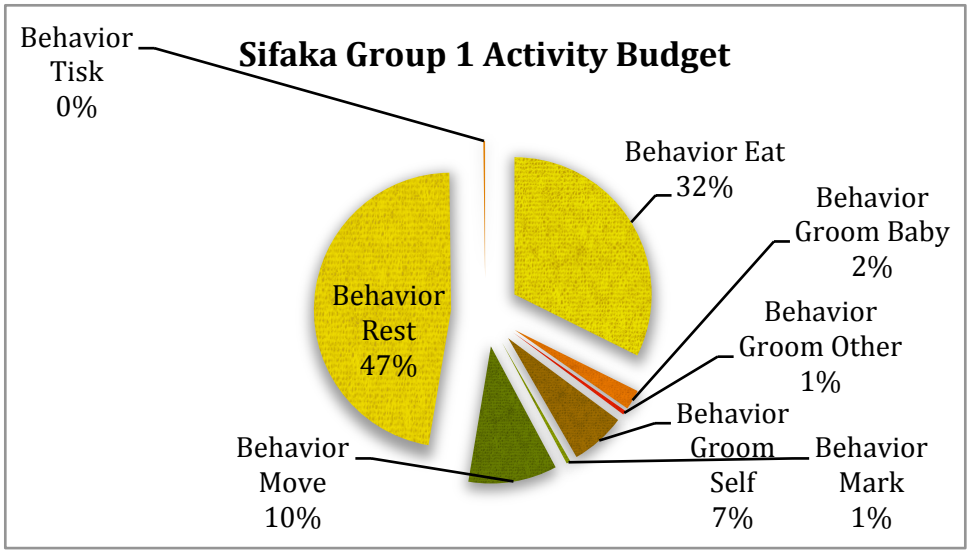


Figure 6.1 Sifaka group 1 activity budget

FEEDING BEHAVIORS BY SIFAKA GROUP 1

Types of foods consumed by sifaka

Out of the total amount of time spent engaged in feeding behavior the sifaka spent the most time feeding on flowers (mainly of the mampay tree) (19.1%) and leaves (43.3%) (Table 6.1).

Table 6.1 Foods consumed by sifaka group 1

Food (N=466)	Total Count	Percentage
Epiphytes	11	2.4%
Fruit	26	5.6%
Flowers	89	19.1%
Mature Leaves	202	43.3%
Seeds	57	3.9%
Young Leaves	77	5.3%
Leaf Stem	4	0.8%

Postural modes used for the consumption of different food items

The sifaka in group 1 displayed a variety of different postures for the consumption of different food items (Table 6.2). The most common posture for eating was a sit (40.8%) followed by a sit-extend (25.0%) (Table 6.2).

Table 6.2 Postures used for food consumption by sifaka group 1

Position (N=466)	Total Count	Percentage	Food eaten in position[13]	Percentage
Recline	33	7.1%	EYL, EL, EFL	54.5%, 24.2%, 21.2%
Sit Extend	116	25.0%	EF, EFL, EL, ES, EYL	2.3%, 6.9%, 51.7%, 12.9%, 22.4%
Sit	190	40.8%	EE, EF, EFL, EL, ES, EYL	5.8%, 6.3%, 23.2%, 43.2%, 15.3%, 6.3%
Stand	8	1.7%	EFL, EL	37.5%, 62.5%
Suspend	69	14.9%	EF, EFL, EL, ES, EYL	8.7%, 34.8%, 33.3%, 15.9%, 7.2%
Vertical Cling	50	10.7%	EF, EFL, EL, ES EYL	10%, 6%, 48%, 4%, 32%

Size of substrate used by sifaka while feeding

Small sized substrates (1-5 cm dbh) were the most common overall supports used by the sifaka in their daily activities (51.0%). Small substrates were also the most commonly used while feeding (52.6%) by the sifaka in group 1 (Table 6.3).

Table 6.3 Size of substrate used for feeding by sifaka group 1

Size of Substrate Used in Feeding	Percentage of Use	Count
Very Small (<1cm)	10.8%	50
Small (1-5 cm)	52.6%	247
Medium (6-10cm)	30.5%	141
Large (11-15 cm)	6.1%	28
Total	100%	466

[13] EYL=eat young leaves, EL=eat leaves, EFL=eat flowers, EF=eat fruit, ES=eat seeds, EE=eat epiphyte.

Height of substrate used by sifaka while feeding

Most of the feeding by sifaka in group 1 took place at a height of 9-10 meters (25.0%) and 11 meters (26%) although all levels were used (Table 6.4). The main foods eaten at these two heights were fruits (10.3%), flowers (26.7%), and leaves (54.3%) at 9-10 meters and flowers (30.3%), seeds (19.7%), and young leaves (23.0%) at 11 meters.

Table 6.4 Height of substrate used for feeding by sifaka group 1

Height of Substrate Used in Feeding (N=466)	Total Count	Percentage of Use
A (1 m)	11	2.3%
B (2-3 m)	10	2.1%
C (4-5 m)	35	7.5%
D (6 m)	34	7.3%
E (7-8 m)	70	15.0%
F (9-10 m)	116	24.9%
G 11 (m)	122	26.2%
H (12-13 m)	61	13.1%

Orientation of substrate used by sifaka during feeding?

Oblique substrates were the most common overall orientation of substrate used by sifaka group 1. Oblique substrates were also the most common substrate used in feeding (47.9%) followed by horizontal substrates (43.2%) and the least used in feeding were vertical substrates (8.9%) (Table 6.5).

Table 6.5 Orientation of substrate used for feeding by sifaka group 1

Food (N=466)	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%
Epiphyte	11	100%	0	0%	0	0%
Fruit	4	15.4%	18	69.2%	4	15.4%
Mature Leaves	87	43.3%	93	46.3%	21	10.4%
Flowers	35	39.3%	53	59.6%	1	1.1%
Seeds	34	59.6%	23	40.3%	0	0%
Young Leaves	28	36.3%	34	44%	15	19.5%

Use of different tree quadrants while feeding by sifaka group 1

Overall, the most common quadrant used by sifaka group 1 was quadrant 6. However, quadrants 2 and 4 were the most used for feeding behavior (Table 6.6). In quadrant 4 sifaka group 1 mainly ate flowers (33.9%) and leaves (26.8%). While quadrant 4 was most commonly used, the sifaka used all quadrants for feeding, including other structures outside of the tree canopy and trunk such as lianas, epiphytes, and ravinala palms (Table 6.6)

Table 6.6 Counts of different food types consumed in designated tree quadrants by sifaka group 1

Food (N)	Quad 1 49	Quad 2 104	Quad 3 49	Quad 4 112	Quad 5 51	Quad 6 59	Quad 7 27	Rav Palm5 2	Epiphyte 3	Liana 20
Epiphyte	0	0	0	11	1	0	0	0	0	0
Fruit	3	7	0	3	7	3	3	0	0	6
Flowers	32	6	3	38	28	2	1	0	0	0
Mature Leaves	3	42	29	30	0	43	15	2	3	7
Seeds	3	29	7	10	5	3	0	0	0	0
Young Leaves	8	20	10	20	10	4	8	0	0	7
Percentage	10.3	21.8	10.3	23.5	10.7	12.4	5.8	0.4	0.6	4.2

Foods consumed in different canopy/vegetation distances by sifaka group 1

Sifaka group 1 engaged in feeding behavior more frequently in connected canopy (Table 6.7). The types of food eaten in this connected layer consisted of all food types except for epiphytes and leaf stems (Table 6.7). The most commonly used foods in this layer were leaves and young leaves (Table 6.7). Importantly, this table shows that sifaka had the flexibility to forage within varying degrees of canopy connectedness. As such, the sifaka adapted their behavior to the distribution of foods, including areas where the foods grow in habitat with more pronounced gaps. The focus on flowers in canopy layers that have small to medium gaps may be attributed to the sifaka eating this food in trees with ample canopy volume that grow some distance from the neighboring tree. The leaves and seeds eaten by sifaka in areas with medium gaps in the canopy may be due to their focus on liana leaves and seeds that tend to grow in open areas (Table 6.7).

Table 6.7 Different canopy distances and different foods consumed by sifaka group 1

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Epiphyte	0 (0%)	11 (14.5%)	0 (0%)	0 (0%)	0 (0%)
Fruit	3 (1.6%)	1 (1.3%)	22 (17.3%)	0 (0%)	0 (0%)
Flowers	43 (22.3%)	0 (0%)	7 (5.5%)	39 (97.5%)	0 (0%)
Mature Leaves	79 (40.9%)	50 (65.8%)	56 (44.1%)	0 (0%)	17 (56.7%)
Leaf Stem	0 (0%)	0 (0%)	4 (3.1%)	0 (0%)	0 (0%)
Seeds	1 (0.5%)	14 (18.4%)	28 (22.0%)	1 (2.5%)	13 (43.3%)
Young Leaves	67 (34.7%)	0 (0%)	10 (7.9%)	0 (0%)	0 (0%)
Total	193 (40.5%)	76 (16.3%)	127 (27.3%)	40 (8.6%)	30 (6.4%)

LOCOMOTION BY SIFAKA GROUP 1

Locomotor modes used by sifaka group 1

There is a difference in time spent resting and moving for sifaka group 1. The sifaka spent more time resting (47.0%) than moving (10.7%) out of their total activity budget. The movement throughout the forest was accomplished through vertical leaps of varying distances. The majority of the leaps were in 1 (37.4%) or 2 (31.6%) meter distances (Table 6.8) with quadrupedal locomotion and leaps of four meters quite rare.

Table 6.8 Locomotor modes used by sifaka group 1

Locomotor Mode (N=155)	Total Count	Percentage
Climb	18	11.6%
L1	58	37.4%
L2	49	31.6%
L3	23	14.8%
L4	2	1.3%
Quadrupedal	1	0.6%
Vertical Bound	4	2.6%

Size of substrate used for locomotion by sifaka group 1

The size of substrate affects movement (K-S, D_{MAX}=0.31, p<0.01). While sifaka in group 1 were capable of utilizing a variety of different sized substrates for movement, including the ground, they focused their movement on medium substrates more so than the other available sizes (51.6%) (Table 6.9).

Table 6.9 Different sized substrates for movement by sifaka group 1

Size of Substrate	Very small	Small	Medium	Large	Ground
Move (N=155)	2 1.3%	59 38.1%	80 51.6%	13 8.4%	1 0.6%

If the correlated behavior "move" is broken down into the various locomotor modes, the main movement by sifaka in group 1 was onto small and medium substrates by leaping one and two meter distances (Table 6.9). The sifaka used a variety of different locomotor modes on small, medium, and large substrates. The only size that was rarely used for movement were the very small substrates or the ground (Table 6.10)

Table 6.10 Different locomotor modes on varying sized substrates used for movement by sifaka group 1

Size of Substrate	Ground	Very Small	Small		Medium		Large	Total
Climb	0	2	6		7		3	18
L1	1	0	32	55.2%	21	36.2%	4	58
L2	0	0	13	26.5%	31	63.3%	5	49
L3	0	0	6		15		2	23
L4	0	0	1		1		0	2
Quadrupedal	0	0	0		1		0	1
Vertical Bound	0	0	0		3		1	4

Heights used for locomotion by sifaka group 1

Height of substrate affects movement (K-S, D_{MAX}=0.17, p<0.01). The main height used for moving by sifaka group 1 was six meters although the sifaka used a variety of heights to move ranging from as low as 1 meter to as high as 13 meters. Leaping one and two meter distances were the common locomotions and occurred at similar heights in the forest. Leaps of one meter were mainly at the height of 6 meters and two meter leaps were made between the heights of 4 and 6 meters (Table 6.11).

Table 6.11 Different heights used for movement by sifaka group 1

Height of Substrate	A	B	C	D	E	F	G	Ground	H	I
Climb	3	0	1	3	4	3	3	0	0	1
L1	7	5	9	16	8	8	3	1	1	0
L2	1	2	13	14	10	8	1	0	0	0
L3	0	0	6	3	7	5	2	0	0	0
L4	0	0	0	2	0	0	0	0	0	0
Quadrupedal	0	0	0	0	0	0	1	0	0	0
Vertical Bound	0	1	0	0	0	2	0	0	1	0
Total	1	8	29	38	29	26	10	1	2	1

Substrate orientations used for different locomotor modes by sifaka group 1

Sifaka primarily used vertical substrates for moving (82.4%) and, albeit to a lesser extent, they also used horizontal (5.9%) and oblique (11.8%) substrates (χ^2=64, df=2, p< 0.001) (Table 6.12). There was an overwhelming use of vertical substrates, and as such, no other apparent preference for different orientations for leaping different distances emerged.

Table 6.12 Locomotor modes used on varying oriented substrates by sifaka group 1

Orientation	Horizontal	Oblique	Vertical
Climb	3	3	12
L1	5	10	42
L2	0	3	46
L3	0	2	21
L4	0	0	2
Quadrupedal	1	0	0
Vertical Bound	0	1	3
Total	9	18	126

Quadrant use for movement by sifaka group 1

Quadrant influences movement (χ^2=729, df= 9, p<0.001). Sifaka group 1 moved through all of the quadrants with a strong preference for quadrant 7 (74.4%) (Table 6.13). The primary locomotor modes the sifaka used in quadrant 7 were 1 and 2 meter leaps. Out of the total number of 1 meter leaps, 67.2% were in quadrant 7. Out of the total number of 2 meter leaps 89.6% were in quadrant 7. Sifaka also were observed moving in lianas and ravinala palms (Table 6.13).

Table 6.13 Movement in varying quadrants by sifaka group 1

Quadrant	1	2	3	4	5	6	7	8	Rav Palm 5	Liana
Move	1	3	1	4	6	10	116	1	4	9

Canopy/vegetation connectivity and locomotor modes by sifaka group 1

The level of connectivity affects movement (K-S, D_{MAX} =0.38, p<0.01). Sifaka in group 1 primarily moved through areas with connected canopy (Table 6.14). The level of connectedness did not affect the locomotor modes used to move through the forest. The sifaka used their full range of leaping distances regardless of the level of connectivity (χ^2=7.36, df=3, p>0.05) (Table 6.15). Overall, the sifaka used between-substrate movement via multiple locomotor modes much more than within-substrate movement, which largely consisted of climbing, short leaps, vertical bounds, and one incident of quadrupedalism (Figure 6.2).

Table 6.14 Different levels of canopy connectedness and movement pattern by sifaka group 1

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Move (N)	86	10	42	4	7

Table 6.15 Different levels of canopy connectedness and locomotor modes used for movement by sifaka group 1

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Climb	9	1	3	0	4
L1	37	2	15	2	2
L2	30	6	10	1	1
L3	10	1	12	0	0
L4	0	0	2	0	0
Quadrupedal	0	0	0	1	0
Vertical Bound	0	0	0	0	0

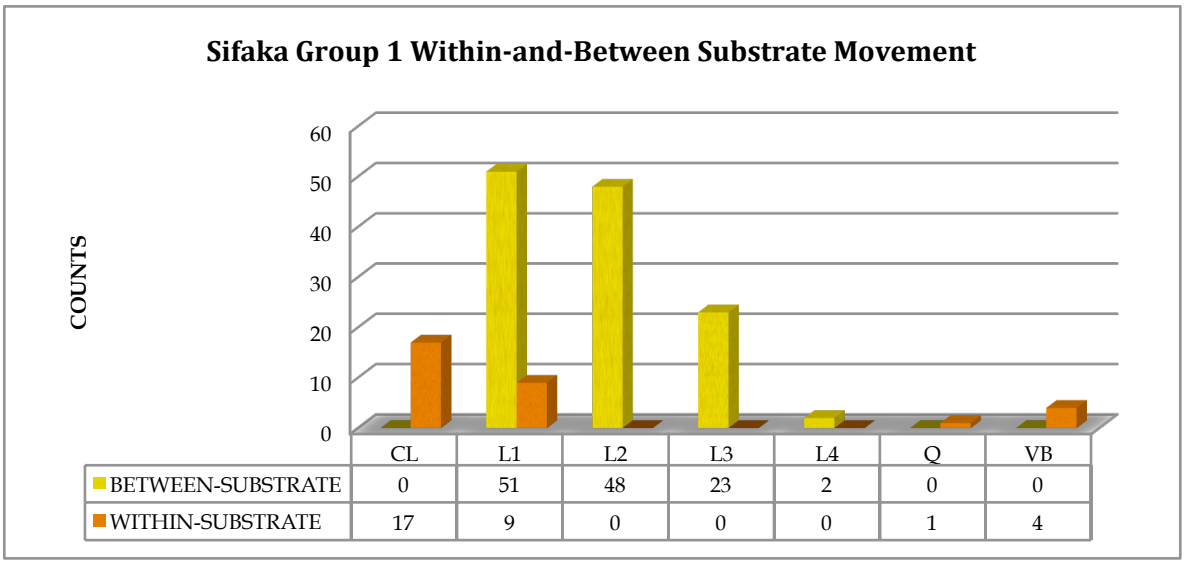


Figure 6.2 Sifaka Group 1 Within-and-Between substrate movement

RESTING BEHAVIORS BY SIFAKA GROUP 1

Postures used for resting by sifaka group 1

Sifaka group 1 spent 47% of their time resting. Sifaka group 1 mainly rested in a sit or sit-extend posture (Table 6.16). Resting while vertical-clinging was often for brief moments, although it could be more extensive, and occurred in the interim between leaps. Often the sifaka took this moment of rest to look around and decide their next leap and route of travel.

Table 6.16 Postural modes used while resting by sifaka group 1.

Positional Activity Rest (N= 677)	Total Count	Percentage
Recline	10	1.5%
Sit-Extend	394	58.2%
Sit	197	29.1%
Stand	2	0.2%
VC	74	10.9%

Size of substrate used for resting by sifaka group 1

Sifaka resting behaviors are not uniformly distributed across substrate sizes (K-S, D_{MAX}=0.27, p<0.01). More than half of the resting behaviors of sifaka group 1 took place on small substrates, although the sifaka were capable of using a variety of different sized substrates for resting behavior (Table 6.17).

Table 6.17 Different sized substrates used for resting behaviors by sifaka group 1

Size of Substrate Resting	Total Count	Percentage
Very Small (<1 cm)	3	0.4%
Small (1-5 cm)	372	54.9%
Medium (6-10 cm)	259	38.3%
Large (11-15 cm)	43	6.4%

Size of substrate used for different resting postural modes by sifaka group 1

While the sifaka preferentially used small substrates for resting, they used the more frequented postures of sit-extend, sit, and vertical-cling (Table 6.18).

Table 6.18 Different sized substrates used for resting postural modes by sifaka group 1

Size of Substrate	Very Small	Small	%	Medium	%	Large	%
Recline	0	6	60%	3	30%	1	10%
Sit-Extend	3	233	59.6%	140	35.8%	18	4.6%
Sit	0	106	53.8%	79	40.1%	12	6.1%
Stand	0	0	0	0	0	2	100%
Vertical Cling	0	327	87.4%	37	9.9%	10	3.1%
Total	3	672		259		43	

Substrate orientation used for resting by sifaka group 1

The orientation of the substrate affects resting behavior (χ^2=214, df=2, p<0.001). While resting, sifaka group 1 spent more time on oblique substrates (Table 6.19).

Table 6.19 Different orientations used in resting behaviors by sifaka group 1

Horizontal Count	%	Oblique Count	%	Vertical Count	%
231	36.2%	379	55.9%	68	10.0%

Height of substrate and resting behavior by sifaka group 1

Sifaka have a preference for resting at certain heights (K-S, D_{MAX}=0.22, p<0.01). Sifaka in group 1 rested at all heights but spent more of their time resting at 9 to 11 meters (28.9%) (Table 6.20).

Table 6.20 Different heights of substrates used in resting behaviors by sifaka group 1

Height of Substrate	A	B	C	D	E	F	G	H
Rest	3 (0.4%)	9 (1.3%)	40 (5.9%)	91 (13.4%)	135 (20.0%)	196 (30.0%)	172 (25.4%)	32 (4.7%)

Quadrant use and resting behavior by sifaka group 1

Sifaka in group 1 preferentially occupy certain quadrants (χ^2=704.3, df=8, p<0.001). Sifaka group 1 rested more frequently in quadrant 6 (43.8%) although all quadrants were used for resting behavior (Table 6.21).

Table 6.21 Different quadrants used in resting behaviors by sifaka group 1

Quadrant	1	2	3	4	5	6	7	Rav Palm 5	Liana
Rest	27 (4.0%)	90 (13.3%)	36 (5.3%)	63 (9.3%)	50 (7.4%)	297 (43.8%)	61 (9.0%)	1 (0.2%)	53 (7.8%)

Canopy/vegetation connectivity and resting behaviors by sifaka group 1

Canopy/vegetation connectedness affects resting behaviors (K-S, D_{MAX}=0.06, p<0.01). The sifaka in group 1 rested more in areas of connected canopy (45.0%) and the least in areas that have small to medium gaps and medium gaps (Table 6.22).

Table 6.22 Distances in canopy used for resting behaviors by sifaka group 1

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	305 (45.0%)	119 (17.6%)	182 (26.8%)	30 (4.4%)	42 (6.2%)

SIFAKA GROUP 1 SUBSTRATE COMBINATIONS AND NEAREST NEIGHBOR

Substrate Combinations

Orientation of substrate and quadrant use by sifaka group 1

Sifaka in group 1 utilized different oriented substrates depending on the quadrant used (Table 6.23). For example, in quadrant 1 the sifaka used horizontal substrates (66.2%) more so than oblique (33.8%). Or, in quadrants 4 (79.3%) and 6 (76.0%) oblique substrates were used more often than either horizontal or vertical. Vertical substrates were used the most in quadrant 7 (94.8%).

Lianas that were oriented horizontally (43.4%), obliquely (28.9%), and vertically (27.7%) were exploited fairly evenly.

Table 6.23 Orientation and quadrant use by sifaka group 1

Quadrant	Horizontal (N)	Oblique (N)	Vertical (N)	Ground (N)
1	51	26	0	0
2	168	42	0	0
3	8	85	0	0
4	39	153	1	0
5	88	39	2	0
6	93	330	11	0
7	3	8	202	0
8	0	0	0	1
Rav Palm 5	0	1	6	0
Epiphyte	3	0	0	0
Liana	36	24	23	0

Height of substrate and quadrant use by sifaka group1

The sifaka in group 1 used a variety of different quadrant and height combinations presented in Table 6.24. Some interesting combinations include the range of heights of liana that sifaka use perhaps giving them more mobility throughout the forest. At lower heights the sifaka had a propensity to use quadrant 7. At taller heights, the sifaka used a range of different quadrants but focused more time in quadrant 6 at the height range of 7 to 10 meters, quadrant 2 and 5 at a height of 11 meters, and quadrants 2 and 3 at a height of 12 to 13 meters.

Table 6.24 Height of substrate and quadrant used by sifaka group 1

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Quad8	Liana	Rav Palm5
A	0	0	0	9	0	1	12	0	2	1
B	0	0	0	2	0	4	11	0	10	0
C	0	0	3	36	0	10	62	0	3	1
D	5	0	4	25	14	59	49	0	10	4
E	0	5	4	11	8	166	44	0	16	1
F	6	72	46	71	11	136	33	0	8	0
G	62	89	4	31	80	48	2	0	34	0
Ground	0	0	0	0	0	0	0	1	0	0

H	4	38	32	6	16	10	1	0	0	0
I	0	6	0	2	0	0	0	0	0	0

Total tree height and height of substrate used by sifaka group 1

Table 6.25 demonstrates that sifaka often chose to engage in behaviors at a height right below the total height of the tree or the actual total height of the tree. The height of the substrate used by the sifaka would also be the total height of the tree. Sifaka in group 1 often sat in trees that have tall slender trunks and narrow canopy widths such that the sifaka body consumed the entire volume of the tree's foliage. However, the total tree height did not seem to influence the height used by the sifaka due to the different combinations of height of substrate and height of tree.

Table 6.25 Height of substrate and total height of tree used by sifaka group 1

Height of tree	B	C	D	E	F	G	GROUND	H	I
Height of Substrate									
A	1	2	1	15	6	0	0	0	0
B	1	8	0	2	9	0	0	7	0
C	0	1	4	55	45	10	0	0	0
D	0	0	8	45	92	21	0	3	1
E	0	0	0	47	147	62	0	2	0
F	0	0	0	1	148	221	0	13	0
G	0	0	0	0	0	205	0	143	2
Ground	0	0	0	0	0	0	1	0	0
H	0	0	0	0	0	0	0	101	6
I	0	0	0	0	0	0	0	0	8

Keystone Structures

Vegetation plots were quantified in the areas repeatedly utilized by the sifaka. In each of these plots trees that were used multiple times were flagged in order to assess the importance of keystone structures in each of these areas. The sifaka used a variety of different forest types ranging from areas with dense understory and a lower canopy to areas of primary rainforest with trees at a height of 14 meters. The canopy/vegetation in the quantified plots that the sifaka used a

number of times was connected in the lower levels and medium-gapped in areas of taller canopy. There were a number of important keystone structures used by the sifaka. Sifaka group 1 mainly focused on keystone feeding trees while resting and moving trees remained more variable. These structures are presented in Table 6.26.

Table 6.26 Keystone structures used by sifaka group 1

Tree Name	Dbh (cm)	Height (m)	Activity	GPS[14]
Hazoambovahy	52	11.9	Feeding leaves	0309317, 8019023
Somotrorana	34	11.3	Feeding fruit	0309370, 8019214
Rotra	34	12.5	Feeding leaves	0309556, 8019141
Dongavelona	42	10.3	Feeding flowers	0309631, 8019228
Hazoambovahy	52	13.0	Feeding leaves	0309694, 8019119
Vongo	7	6.9	Feeding leaves	0309660, 8019888

SIFAKA GROUP 1 NEAREST NEIGHBOR

Identity of nearest neighbor

When the radio-collared female was the focal animal, the nearest neighbor was mostly (73%) at least 20 meters away (Table 6.27). The focal adult female spent a majority of her time alone. When she was near the other members of her group the nearest neighbor was the other female 37.5% of the time and the adult male 41.6% of time.

Table 6.27 Nearest neighbors to focal sifaka female group 1

Adult Female	Adult Male	Male/Female	> 20 meters away
110	122	61	792

[14] Latitude and longitude recorded from GPS unit. This recording will allow the trees to be located in the future.

Distance of nearest neighbor

The most common distance for the sifaka group spacing from the focal animal was more than 20 meters. When they were closer in proximity, the focal female and the nearest neighbor female would be in contact (33.6%) and the adult male would commonly be 1 meter away (33.6%) from the focal female (Table 6.28).

Table 6.28 Distances of nearest neighbors to sifaka female in group 1

Distances (m)	0	1	2	3	4	5	8	10	>20
Adult Female (N)	37	22	11	30	7	2	0	1	0
Adult Male (N)	24	41	11	8	4	10	0	24	0
Male/Female (N)	2	0	8	4	11	4	11	21	0
>20 (N)	0	0	0	0	0	0	0	0	792

Sifaka Group 1 Summary Statement:

Microhabitat features influenced sifaka group 1 movement, feeding, and resting behaviors. These paragraphs highlight those substrates the sifaka utilized at a higher frequency than others, but as noted in the preceding sections, sifaka in group 1 were capable of utilizing a wide range of different heights and substrates for resting, eating, and moving. Overall sifaka in group 1 frequently used small, oblique substrates at a height of 9 to 11 meters in quadrant 6. The total main canopy height the sifaka used also was at a height between 9 and 11 meters.

Sifaka in group 1 spent a majority of their activity budget resting and 32% of their time feeding. The sifaka's microhabitat use reflected the characteristics of the food sources they were eating. Feeding behavior and subsequent substrate choice was most likely driven by the way the foods in the forest are distributed and was therefore difficult to evaluate with hypotheses testing. Despite this some interested patterns emerged discussed below.

The sifaka ate a broad range of different foods with the most focus on flowers and mature and young leaves. While eating, the sifaka assumed a sit-posture on small branches at heights between 9 and 11 meters. The sifaka used oblique and horizontal substrates in quadrant 4 for feeding behaviors. The keystone trees for the sifaka in group 1 consisted of important feeding trees that were used on a regular basis. In contrast, the sifaka used a variety of different substrates for moving and resting with no attachment or redundant use of certain substrates for these behaviors. During each all-day follow, the trees were flagged that the sifaka moved, fed, and rested in and were identified if possible. A table of the trees used by the sifaka in group 1 is listed in the appendix. The top five trees used by sifaka group 1 for all behaviors include liana (N=11), mampay (N=9), rara (N=8), hazoambovahy (N=6), and somotrorana (N=6).

Sifaka in group 1 used one and two meter leaps to move through the forest. The sifaka were capable of using a variety of different sized substrates including the ground for movement, but the majority of the leaping bouts occurred on medium vertical substrates. The only size rarely used for movement was very small sized substrates. The sifaka also used a variety of heights for movement, although the most frequented height was four to six meters in quadrant 7. Sifaka also made use of lianas and ravinala palms for movement. A majority of the locomotion for the sifaka was through areas with connected canopy/vegetation. The level of connectedness did not affect the locomotor mode used to move through the forest. The sifaka used their full range of leaping distances regardless of the level of connectivity. Overall, the sifaka used between-substrate movement via multiple locomotor modes much more than within-substrate movement, which largely consisted of climbing, short leaps, and vertical bounds.

Sifaka group 1 spent a greater proportion of their time resting than in other activities. The sifaka mainly rested in connected canopy assuming a sit-extend or vertical-cling posture on small oblique substrates at a height of 9 to 11 meters in quadrant 6.

The sifaka in group 1 utilized different oriented substrates depending on the quadrant used. For example, when the sifaka were using quadrants 1, 2, or 5 they tended to use horizontal substrates. In quadrants closer to the main trunk of the tree (i.e. quadrants 4 and 6) the sifaka used oblique more often than horizontal or vertical substrates. When the sifaka made use of the lianas, they used all three orientations relatively equally.

The height of the substrate used by the sifaka was often the same height of the tree. For example, sifaka often sat in trees that had tall slender trunks and narrow canopy widths such that the sifaka's body consumed the entire volume of the tree's foliage. Sifaka focused their use on trees 9 to 11 meters in total height, but also used a wide range of different substrate and tree height combinations.

In sum, sifaka in group 1 were quite flexible in their ability to use a wide range of different substrates, orientations, and heights for resting, feeding, and moving behaviors. The sifaka appeared to have a heightened preference for certain substrates but were also quick to use others when their preference was unavailable.

The radio-collared female was rarely in close proximity to the other group members during the day. But rather, reconvened with her other group members in the evenings in their sleeping trees. When the group traveled together, the focal female was around the male just as much as she was around the other female in the group. When the group split during the day, the radio-collared female was always the lemur that was followed so it remains unknown if the other two group members traveled together or if they too separated. This creates a niche for future research in developing a more detailed study of resource availability for this group.

Subsection 6.2
***EULEMUR* GROUP 34**

EULEMUR GROUP 34: Group composition consisted of one adult female (Harriet) and two juvenile males. One juvenile appeared to be younger (Oliver) than the other (Stuart) based on body size and also dependency to the adult female in the form of close spatial proximity.
Female radio collar. 2.5kg, body length 34.6cm, tail length 53.9cm
Males no collar. Not captured.

Summary of substrate use and total activity budget for *Eulemur*
Overall size of substrate: A 13.9%, B 57.9%, C 27.0%, D 1.1%
Overall height of substrate: A 0.5%, B 1.5%, C 3.7%, D 7.5%, E 28.7%, F 28.9%, G 23.3%, H 5.9%
Overall quadrant: Quad1 7.8%, Quad2 3.1%, Quad3 18.5%, Quad4 11.9%, Quad5 31.1%, Quad6 17.3%, Quad7 2.1%, Quad8 0.1%, RavPalm 5 0.9%, Rav Pod6 2.2%, Liana 4.2%, Liana Tangle 1.0%
Overall orientation: A 36.3%, B 62.1%, C 1.6%
Total activity budget: Eat fruit 9.2%, Eat flowers 6.0%, Eat leaves 2.6%, Eat nectar 3.7%, groom other 2.9%, Groom-self 6.3%, Move 9.7%, Rest 59.2%, Threat 0.4%
Total tree height: A 0.2%, B 0.3%, C 3.6%, D 2.1%, E 6.3%, F 38.4%, G 34.5%, H 14.4%, I 0.2%

The female was the only individual of the three to be darted and fitted with a radio-collar. The female appeared to be in good health. This group used a small central portion of the reserve as their home range. This group spent 23.8% of the time eating, 10.0% of the time moving, and 59.0% of the time resting (Figure 6.3).

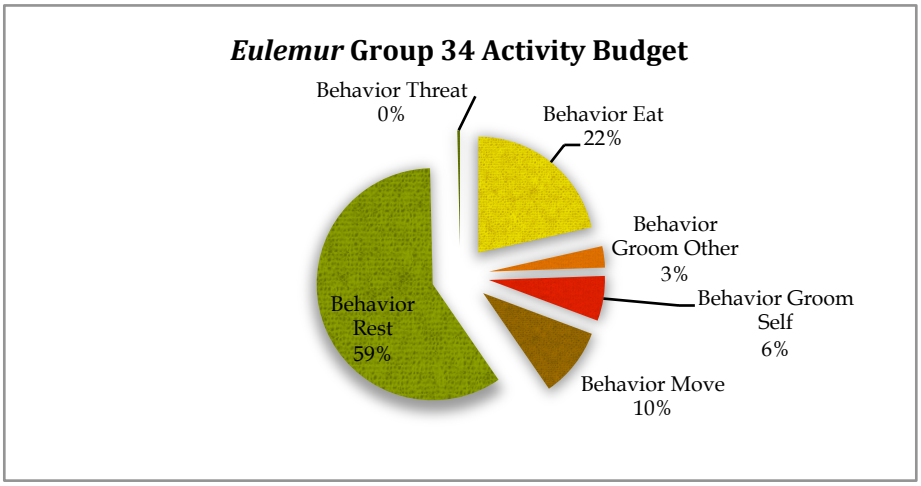


Figure 6.3 *Eulemur* group 34 activity budget

FEEDING BEHAVIORS BY EULEMUR GROUP 34

Types of foods consumed by brown lemur group 34

Out of the total amount of time spent engaged in feeding behavior the brown lemurs spent the most time feeding on fruit (42.7%) and flowers (27.9%) (Table 6.29).

Table 6.29 Foods consumed by *Eulemur* group 34

Food (N=405)	Total Count	Percentage
Fruit	173	42.7%
Flowers	113	27.9%
Mature Leaves	49	12.1%
Nectar	70	17.3%

Postures used for the consumption of different foods by brown lemur group 34

Brown lemurs in group 34 displayed a variety of different postures for the consumption of different food items (Table 6.30). The most common posture for eating was standing (43.5%) followed by sitting (43.5%) (Table 6.30).

Table 6.30 Postures used for food consumption by *Eulemur* group 34

Posture (N=405)	Total Count	Percentage	Food eaten in posture	Percentage
Recline	1	0.2%	EF	100%
Sit Extend	2	0.5%	EF	100%
Sit	176	43.5%	EF, EFL, EL, LFL[15]	48.3%, 22.7%, 15.3%, 13.6%
Stand	204	50.4%	EF, EFL, EL, LFL	38.2%, 30.4%, 10.8%, 20.6%
Sit Tail Wrap	5	1.2%	EF, LFL	80%, 20%
Suspend	16	4.0%	EF, EFL, LFL	18.8%, 62.5%, 18.8%
Vertical Cling	1	0.2%	EF	100%

[15] LFL=eat flower nectar

Size of substrate used by brown lemur group 34 while feeding

Small sized substrates (1-5 cm dbh) were the most common overall supportive material the brown lemurs used in their daily activities. This use of small substrates was also a common sized substrate (42.7%) along with very small substrates (48.6%) used in their feeding behavior. When each type of food the brown lemurs ate is broken down into its separate categories, the result is still an emphasis on utilizing very small and small substrates when eating all food items (Table 6.31).

Table 6.31 Size of substrate used for food consumption by *Eulemur* group 34

Size of Substrate Used in Feeding	Percentage of Use
Very Small (<1 cm)	48.6%
Small (1-5 cm)	42.6%
Medium (6-10 cm)	8.6%
Large (11-15 cm)	0%

Height of substrate used by brown lemur group 34 while feeding

Eulemur group 34 primarily used the heights of 7 to 11 meters for most of their daily activities. Most of the feeding by *Eulemur* group 34 took place at a height of 9 to10 meters (33.8%) although all levels were used (Table 6.32). The main foods eaten at this height were fruit (35.8%), flowers (21.2%), nectar (28.5%) and leaves (14.6%).

Table 6.32 Height of substrate used for food consumption by *Eulemur* group 34

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	2	0.5%
B (2-3 m)	15	3.7%
C (4-5 m)	6	1.5%
D (6 m)	46	11.3%
E (7-8 m)	83	20.5%
F (9-10 m)	137	33.8%
G 11 (m)	84	20.7%
H (12-13 m)	32	7.9%
I (14-15 m)	0	0

Orientation of substrate used by brown lemur group 34 while feeding

Oblique substrates were the most common overall orientation of substrate used by the brown lemur group (62.1%). Oblique substrates were also the most common substrate used in feeding (71.4%) followed by horizontal substrates (28.7%). *Eulemur* did not use vertical substrates in any feeding behavior. While eating fruits, flowers, and leaves, the brown lemurs used a higher percentage of oblique substrates. While eating nectar the brown lemurs spent equal portions of time using oblique (51.4%) and horizontal (48.6%) substrates (Table 6.33).

Table 6.33 Orientation of substrate used for food consumption by *Eulemur* group 34

Food	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%
Fruit	37	21.4%	136	78.6%	0	0
Mature Leaves	13	26.5%	36	73.5%	0	0
Flowers	32	28.3%	81	71.7%	0	0
Nectar	34	48.6%	36	51.4%	0	0

Use of different tree quadrants while feeding by brown lemur group 34

Overall, the most common quadrant used by the brown lemurs was quadrant 5. Quadrant 5 was also the most used quadrant (23.7%) for feeding behavior followed by quadrant 1 (20.5%) (Table 6.34). The brown lemurs focused on fruits (56.7%) while occupying quadrant 1, whereas flowers, fruit, and nectar were the main focus in quadrant 5.

Table 6.34 Quadrant used for food consumption by *Eulemur* group 34

Food	Quad 1 (N=83)	Quad 2 (N=34)	Quad 3 (N=72)	Quad 4 (N=63)	Quad 5 (N=96)	Quad 6 (N=44)	Quad 7 (N=4)	Rav Palm5 (N=1)	Liana Tangle (N=8)
Fruit	47	14	37	16	29	23	2	1	4
Flowers	18	7	26	20	35	4	0	0	3
Mature Leaves	13	11	0	10	4	8	2	0	1
Nectar	5	2	9	17	28	9	0	0	0

Foods consumed in different levels of canopy/vegetation connectivity by brown lemur group 34

The brown lemurs primarily foraged for food in connected canopy (41.5%). They also foraged for food in areas where the canopy had small gaps (30.4%). Interestingly, the lemurs foraged for food more frequently in areas where the canopy had medium gaps (24.4%) rather than connected/small gaps (3.7%). Flowers were the main food eaten in connected canopy/vegetation areas (61.9%) with less focus on areas where the canopy had small (5.7%) or medium gaps (2.0%) (Table 6.35). A majority of the fruit was eaten in areas where the canopy had medium gaps (98.0%). Flowers were never eaten in areas where the canopy had connected and small gaps or small to medium gaps. This most likely is attributed to the natural distribution of foods throughout the forest, which brown lemurs then adjusted their feeding behavior.

Table 6.35 Different canopy/vegetation distances and foods consumed by *Eulemur* group 34

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Eat Fruit	33 (19.6%)	11 (73.3%)	32 (26.0%)	0 (0%)	97 (98.0%)
Eat Flowers	104 (61.9%)	0 (0%)	7 (5.7%)	0 (0%)	2 (2.0%)
Eat Leaves	31 (18.5%)	4 (26.7%)	14 (11.4%)	0 (0%)	0 (0%)
Eat Nectar	0 (0%)	0 (0%)	70 (56.9%)	0 (0%)	0 (0%)
Total	168	15	123	0	99

LOCOMOTION BY EULEMUR GROUP 34

Locomotor modes used by brown lemur group 34

There was a difference in time spent resting and moving for *Eulemur* in group 34. *Eulemur* spent more time resting (59.0%) than moving (10%) out their total activity budget. This movement throughout the forest was accomplished through leaps of varying distances (Table 6.36) although the majority of the movement was through quadrupedal locomotion (60.9%). When leaping,

Eulemur tended to focus on shorter distance leaps of ≤1 meter instead of two to three meter leaps (Table 6.36).

Table 6.36 Locomotor modes used by *Eulemur* group 34

Locomotor Mode (N=184)	Total Count	Percentage
Climb	10	5.4%
L<1	27	14.7%
L1	21	11.4%
L2	6	3.3%
L3	3	1.6%
Quadrupedal	112	60.9%
Vertical Bound	5	2.7%

Size of substrate used for locomotion by brown lemur group 34

Size of substrate affects brown lemur movement (K-S, D_{MAX}=0.21, p<0.01). *Eulemur* spent a majority of their moving behaviors on small substrates. Despite the main focus on small substrates, brown lemurs were also quite capable of using very small and medium branches, but rarely used large substrates (Table 6.37)

Table 6.37 Different sized substrates for movement by *Eulemur* group 34

Size of Substrate	Very small	Small	Medium	Large	Ground
Move (N=183)	39 21.3%	80 43.7%	57 31.1%	7 3.8%	0

If the correlated behavior "move'" is broken down into the various locomotor modes, the brown lemurs moved by quadrupedal locomotion more so on small substrates (Table 6.38). Outside of quadrupedal locomotion, leaping was the primary mode of locomotion on very small and small substrates. Less focus was dedicated to medium substrates and no time was spent moving on large substrates. When leaping greater distances the brown lemurs used larger diameter substrates as their target material.

Table 6.38 Different locomotor modes on varying sized substrates by *Eulemur* group 34

Size of Substrate	Ground	Very Small	Small	Medium	Large
Climb	0	2	6	1	0
L<1	0	12	13	2	0
L1	0	5	8	7	1
L2	0	0	1	5	0
L3	0	0	0	3	0
Quadrupedal	0	20	50	36	6
Vertical Bound	0	0	2	3	0

Heights used by brown lemur group 34 for locomotion

Height of substrate affects movement (K-S, D_{MAX}=0.12, p<0.01). The overall main height for movement was between 7 to 8 (30.4%) and 9 to 10 (24.3%) meters. Brown lemurs were not completely limited by height for their movement patterns and different types of locomotion occurred throughout a wide range of heights (Table 6.39).

Table 6.39 Different heights used for movement by *Eulemur* group 34

Height of substrate	A	B	C	D	E	F	G	H
Climb	0	0	0	1	4	2	2	0
L<1	2	0	0	4	8	8	5	0
L1	1	0	1	4	3	10	2	0
L2	0	1	1	1	3	0	0	0
L3	0	1	0	0	0	2	0	0
Quadrupedal	3	3	6	13	37	22	24	4
Vertical Bound	0	0	2	1	2	0	0	0

Substrate orientations used for different locomotor modes by brown lemur group 34

Orientation of substrate influences movement (χ^2=28.5, df=2, p<0.01). *Eulemur* mainly used oblique (48.1%) substrates followed by horizontal (36.0%) and then vertical (15.8%) for moving. Quadrupedal locomotion was conducted on horizontal and oblique substrates an equal proportion of time. Most of the leaping occurred on oblique substrates as well (Table 6.40).

Table 6.40 Locomotor modes used on varying oriented substrates by *Eulemur* group 34

Orientation	Horizontal	Oblique	Vertical
Climb	2	2	6
L<1	1	21	5
L1	4	13	4
L2	0	1	5
L3	0	0	3
Quadrupedal	59	50	3
Vertical Bound	0	2	3

Quadrant use for movement by brown lemur group 34

Eulemur have a preference for certain quadrants for movement (χ^2=28.6, df=6, p<0.001). When moving, *Eulemur* used all of the quadrants to some degree but mainly used quadrant 5 (29.5%) (Table 6.41). The primary mode of locomotion the brown lemurs used in this quadrant was quadrupedal walking and running.

Table 6.41 Movement in varying quadrants used by *Eulemur* group 34

Quadrant	1	2	3	4	5	6	7	8	Rav Palm 5	Liana	Liana Tangle
Move (N)	6	4	29	23	40	26	20	1	2	27	5

Canopy/vegetation connectivity and locomotor modes by brown lemur group 34

Canopy/vegetation connectedness affects brown lemur movement (K-S, D_{MAX}=0.15, p<0.01). *Eulemur* mainly moved through connected forest although they were also capable of moving through forest of varying degrees of openness including areas with medium gaps (Table 6.42). Quadrupedal locomotion was the most common form of locomotion within all canopy distances. Canopy connectedness also affected locomotor modes (χ^2=24.4, df= 4, p<0.001). The brown lemurs tended to leap more in areas of connected canopy and used quadrupedal locomotion for all levels of connectedness (Table 6.43). Overall, the brown lemurs used between-substrate movement (64.6%) more so than within substrate movement (35.4%). Between-substrate movement

consisted of a variety of different locomotor modes whereas within-substrate locomotion largely consisted of quadrupedal locomotion (Figure 6.4).

Table 6.42 Levels of canopy connectedness used for movement by *Eulemur* group 34

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Move (N)	93	25	47	1	17

Table 6.43 Levels of canopy connectedness and locomotor modes by *Eulemur* group 34

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Climb	6	1	2	0	0
L<1	12	9	6	0	0
L1	12	0	8	0	1
L2	3	2	1	0	0
L3	0	0	1	0	2
Quadrupedal	57	12	28	1	14
Vertical Bound	0	0	0	0	0

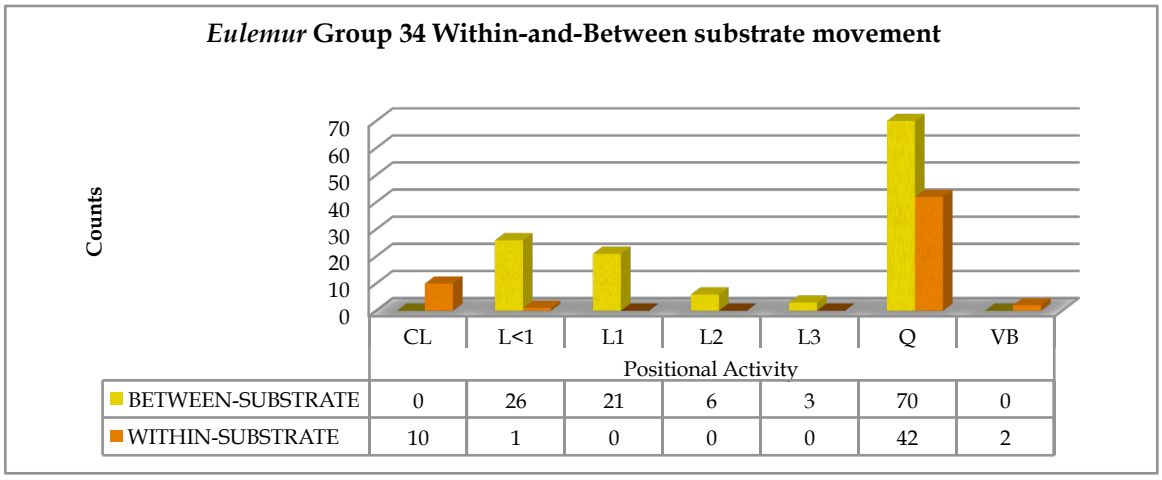


Figure 6.4 *Eulemur* group 34 within-and-between substrate movement

RESTING BEHAVIORS BY *EULEMUR* GROUP 34

Postures used for resting by brown lemur group 34

Eulemur group 34 spent 59.0% of the time out of their total activity budget resting. *Eulemur* mainly rested in the sit-tail wrap posture (80.4%) (Table 6.44).

Table 6.44 Postural modes used while resting by *Eulemur* group 34

Postural Modes for Rest (N= 1117)	Total Count	Percentage
Sit-tail wrap	898	80.4%
Sit-Extend	12	1.1%
Sit	172	15.4%
Stand	31	2.8%
Vertical Cling	4	0.4%

Size of substrate used for resting by brown lemur group 34

Brown lemurs prefer to rest on small substrates (K-S, D_{MAX}=0.24, $p<0.01$). More than half of the resting behaviors of *Eulemur* group 34 took place on small substrates although brown lemurs were capable of using a variety of different sized substrates (Table 6.45).

Table 6.45 Different sized substrates used for resting behaviors by *Eulemur* group 34

Size of Substrate Resting	Total Count	Percentage
Very Small (<1 cm)	25	2.2%
Small (1-5 cm)	704	63.0%
Medium (6-10 cm)	383	34.3%
Large (11-15 cm)	5	0.4%

Size of substrate used for different resting postural modes by brown lemurs group 34

When resting in a tail wrap posture, *Eulemur* group 34 mainly used small substrates but also medium substrates (Table 6.46). The brown lemurs rarely used large-sized substrates for any resting position.

Table 6.46 Different sized substrates used for resting postures by *Eulemur* group 34

Size of substrate	Very small	%	Small	%	Medium	%	Large	%
Sit-Extend	0	0%	10	83.3%	2	16.7%	0	0%
Sit	8	4.7%	106	61.6%	57	33.1%	1	0.6%
Stand	4	12.9%	14	45.2%	11	35.5%	2	6.5%
Sit tail wrap	13	1.5%	574	63.9%	309	34.4%	2	0.2%
Vertical Cling	0	0%	0	0%	4	100%	0	0

Substrate orientation used for resting by brown lemur group 34

Eulemur have a preference for certain substrate orientations for resting behaviors (χ^2=644, df=2, p<0.001). *Eulemur* in group 34 spent more time resting on oblique substrates (61.7%) (Table 6.47).

Table 6.47 Different orientations used for resting behaviors by *Eulemur* group 34

Horizontal Count	%	Oblique Count	%	Vertical Count	%
426	38.1%	689	61.7%	2	0.2%

Height of substrate and resting behavior by brown lemur group 34

Brown lemurs have a preference for resting at certain heights (K-S, D_{MAX}=0.32, p<0.01). *Eulemur* rested at a variety of different heights including much lower in the canopy at a height of two to four meters all the way up to a height of 12 to 13 meters (Table 6.48). However, the brown lemurs rested more frequently at a height ranging between seven and eleven meters (Table 6.48).

Table 6.48 Height of substrate used while resting by *Eulemur* group 34

Height of Substrate	A	B	C	D	E	F	G	H
Rest	1	9	47	66	349	300	277	68

Quadrant use and resting behavior by brown lemur group 34

Quadrant use influences rest (χ^2=1083, df=8, p<0.01). *Eulemur* used a variety of different quadrants for rest, including ravinala palms and seed pods, and lianas. *Eulemur* spent the majority of their resting time lower in the canopy in the periphery branches in quadrant 5 (35.9%) (Table 6.49).

Table 6.49 Different quadrants used for resting by *Eulemur* group 34

Quadrant	1	2	3	4	5	6	7	Rav Palm5	Liana	Rav Pod6	Liana Tangle
Rest	51	20	207	113	401	222	12	4	46	35	6

Canopy/vegetation connectivity and resting behaviors by brown lemur group 34

Canopy/vegetation connectivity affects resting behavior (K-S, D_{MAX}=0.11, p<0.01). *Eulemur* frequently rested in connected canopy (49.5%). The brown lemurs also had the ability to rest within a range of different canopy distances (Table 6.50). The degree of connectedness the brown lemurs were not observed to use were areas containing small-medium gaps. This may reflect the forest types the brown lemurs were using and not necessarily the inability to use this category of connectedness, because brown lemurs were observed to rest in areas with medium gaps. Interestingly, brown lemurs also frequently rested in areas with medium gaps in the canopy even more so than in areas with connected/small gaps and small gaps (Table 6.50).

Table 6.50 Distances in canopy connectivity used for resting behaviors by *Eulemur* group 34

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	405	148	249	0	315

EULEMUR GROUP 34 SUBSTRATE COMBINATIONS AND NEAREST NEIGHBOR

Substrate Combinations
Orientation of substrate and quadrant use by brown lemur group 34

In every quadrant brown lemurs used oblique substrates more frequently than either horizontal or vertical substrates (Table 6.51). The exceptions to this include their use of ravinala palms and lianas where horizontal substrates were used more frequently (Table 6.51). Vertical substrates were only used in quadrant 7, or the tree trunk, and some lianas.

Table 6.51 Orientation and quadrant use by *Eulemur* group 34

Quadrant	Horizontal	Oblique	Vertical
1	30	115	0
2	3	55	0
3	108	240	0
4	64	156	4
5	246	340	0
6	148	176	2
7	3	16	20
8	0	2	0
Rav Palm 5	16	2	0
Rav Pod 6	0	42	0
Liana	62	12	5
Liana Tangle	4	15	0

Height of substrate and quadrant use by brown lemur group 34

For all quadrants, the brown lemurs used oblique substrates more frequently. The exceptions to this include the use of lianas and ravinala palms, in which case, horizontal substrates were used more often. The brown lemurs used lianas and liana tangles primarily below a height of seven meters. The use ravinala palms and seed pods was at a height of 11 meters due to the overall height and growth patterns of the ravinala trees. There appears to be no pattern in brown lemur behavior in their choice of central of peripheral positioned quadrants in relation to heights used for resting, moving, and feeding behaviors (Table 6.52).

Table 6.52 Height of substrate and quadrant use by *Eulemur* group 34

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Liana	Rav Palm5	Rav Pod6	Liana Tangle
A	0	0	0	0	0	1	0	0	0	0	0
B	0	0	0	0	0	2	1	0	0	0	3
C	0	0	0	15	0	0	0	38	1	0	10
D	10	0	0	3	0	2	3	13	2	0	1
E	9	0	4	4	0	43	7	15	0	0	5
F	40	29	152	76	261	145	14	7	0	0	0
G	62	29	121	91	0	111	3	5	15	42	0
H	24	0	71	35	0	22	11	1	0	0	0
I	0	0	0	0	0	0	0	0	0	0	0

Total tree height and height of substrate used by brown lemur group 34

The height of the substrate used by the brown lemurs was often the total height of the tree indicating that the brown lemurs frequented trees with small canopy volume (Table 6.53). However, the brown lemurs also used substrates in trees with wide canopy volume indicated by the height of the substrate used and overall canopy height.

Table 6.53 Height of substrate and total height of tree used by *Eulemur* group 34

Height of tree	A	B	C	D	E	F	G	H	I
Height of Substrate									
A	2	1	2	2	2	0	0	0	0
B	1	3	8	4	3	10	0	0	0
C	0	0	58	6	2	3	0	0	0
D	0	2	0	25	78	33	0	4	0
E	0	0	0	0	33	491	16	1	0
F	0	0	0	1	1	187	348	8	0
G	0	0	0	0	0	0	287	152	0
H	0	0	0	1	0	0	0	107	4

Keystone Structures

Vegetation plots were quantified in the areas repeatedly utilized by the brown lemurs. In each of these plots trees that were used multiple times were flagged in order to assess the importance of keystone structures in each of these areas. The brown lemurs frequently used space

that was crowded with tree falls, dead fallen and standing trees, liana clusters, bamboo tangles, and a low canopy. Their home range also included areas with small pockets of longoza. Keystone structures were identified in several of the plots and are presented in Table 6.54. The important famelona tree the brown lemurs used as a resting tree as well as ate its fruits was located in the middle of a 20 m^2 open tree fall area consumed with longoza, mazomboaty, stinging wasps, and viney bamboo. Yet, the brown lemurs returned to this area quite frequently. Liana clusters or vine tangles inundated with dead leaves also seemed to be important keystone elements for the brown lemurs, especially as points of refuge from other lemur groups or for resting behaviors during torrential down pours.

Table 6.54 Keystone structures used by *Eulemur* group 34

Malagasy Tree	Dbh (cm)	Height (m)	Activity	GPS
Antaifara	42	10.3	Feeding flowers	(0309624, 801835)
Zanamena	18	10.5	Feeding leaves	(0309627, 801839)
Ravinala	28	6.4	Resting	(0309627, 801839)
Ramy	18	9.5	Moving	(0309627, 801839)
Famelona	42	10.8	Feeding fruit	(0309598, 801834)
Mandresy	28	11.1	Feeding fruit	(0309544, 801831)

EULEMUR 34 NEAREST NEIGHBOR

Identity of nearest neighbor

When the radio-collared female was the focal animal the nearest neighbor was most frequently both of the juvenile males (Table 6.55). This brown lemur group was very cohesive and a nearest neighbor was never more than 20 meters away. When the nearest neighbor was just one juvenile instead of the two, this was usually the younger the male. The older juvenile occassionally ventured to the adjacent tree to forage on his own.

Table 6.55 Nearest neighbors to brown lemur female in group 34

1 Juvenile	2 Juveniles	> 20 meters away
183	1703	0

Distance of nearest neighbor

Close proximity (contact or ≤1 meter) was the most common distance to the nearest neighbor within group 34. The younger juvenile was rarely farther than two meters away from the focal female (Table 6.56). The older juvenile was also in close proximity to the focal female rarely venturing out farther than four meters (Table 6.56).

Table 6.56 Distances of nearest neighbors to brown lemur female in group 34

Distances (m)	0	1	2	3	4
1 Juvenile	118	44	20	1	0
2 Juveniles	1352	199	101	49	2

***Eulemur* group 34 Summary Statement:**

Microhabitat features influenced *Eulemur* group 34 movement, feeding, and resting behaviors. These paragraphs highlight those substrates the brown lemurs utilized at a higher frequency than others, but as noted in the preceding sections, brown lemurs in group 34 were capable of utilizing a wide range of different heights and substrates for resting, eating, and moving. Overall, the brown lemurs in group 34 used small, oblique substrates at a height of 7 to 10 meters in quadrant 5 for most activities. The total canopy height of the areas the brown lemurs used was primarily 9 to 11 meters. The brown lemurs spent most of their resting compared to their other daily activities. During each all day follow the trees were flagged that the brown lemurs moved, fed, and rested in and were identified if possible. A table of the trees used by *Eulemur* in group 34 is listed in the appendix. The brown lemurs expressed an affinity for certain keystone structures that were important for resting, feeding, and moving. The lemurs returned to these specific trees on a

regular basis. The top five trees used for resting, feeding, and moving included antafonana (N=5), azinina (N=5), mampay (N=5), ramy (N=5), and famelona (N=4).

The brown lemurs spent a majority of the time eating fruit and flowers by standing and sitting on very small and small, oblique substrates at a height of 9 to 10 meters with this height also broadening out to a range of 7 to 11 meters in some feeding occurrences. The brown lemurs focused on quadrants 1, 3, and 5 in areas with connected canopy and small gaps.

The brown lemurs primarily used quadrupedal locomotion but also moved through the forest via short leaps using very small, small, and medium-sized substrates. Leaps of <1 meter were primarily on very small substrates. Brown lemurs moved mainly by between-substrate movement through connected canopy and often jumped onto the very small perimeter branches of the adjacent tree to move through the forest. If the branches of the adjacent trees were close enough, the brown lemurs also moved by quadrupedal locomotion through the closed canopies using these very small branches. The brown lemurs actively moved through congested, (e.g. tree falls and liana clusters) connected areas of the forest. They rarely used large substrates for movement and they rarely moved at a height greater than 11 meters. Most of their movement was focused at a height between 7 and 11 meters. They mainly used horizontal and oblique substrates for quadrupedal locomotion whereas leaping occurred more frequently on oblique substrates. The lemurs primarily used quadrant 5, but also used quadrants 3, 4, 6, 7, and lianas fairly evenly.

Brown lemurs in group 34 mainly rested by assuming a sit-tail wrap posture on small oblique substrates. The brown lemurs rarely used large substrates for resting. The brown lemurs used the main heights of 7 to 11 meters for resting. *Eulemur* used quadrants in the periphery of the tree (quadrants 3, 5) but also rested closer to the trunk of the tree (quadrant 6) on occassion. These lemurs used other substrates outside of the tree canopy for rest as well, including ravinala seed pods and palm fronds, single lianas, and liana tangles. The brown lemurs frequently rested in areas with connected canopy or medium gaps. These areas with medium gaps can be attributed to

the brown lemurs' affinity for space with tree falls and liana/vine clusters that create gaps in the forest.

For all quadrants, the brown lemurs used oblique substrates more frequently. The exceptions to this include the use of lianas and ravinala palms, in which case, horizontal substrates were used more often. Brown lemurs repeatedly used lianas and liana tangles below the height of seven meters. No pattern emerged in the brown lemur behavior in their choice of centrally or peripherally located quadrants and the corresponding heights. The height of the substrate used by the brown lemurs was often the total height of the tree indicating that the brown lemurs frequented trees with small canopy volume. However, the brown lemurs also used substrates in trees with wide canopy volume indicated by the height of the substrate used and overall canopy height.

When the radio-collared female was the focal animal, the nearest neighbor was most frequently both of the juvenile males. This brown lemur group was very cohesive and a nearest neighbor was never more than 20 meters away. When the nearest neighbor was just one juvenile instead of the two, this was usually the younger the male. The older juvenile ventured off on his own to the adjacent tree, for example, to forage on his own but this distance was never more than four meters.

The brown lemurs appear to have a heightened predilection for certain substrates in their environment but are also quick to use others when these substrates were unavailable. The brown lemurs occupied a small home range and were often supplanted out of their space by other brown lemur groups and by other lemur species (e.g. *Varecia*). This is discussed in more detail in section II that focuses on macrohabitat.

Subsection 6.3
PROPITHECUS GROUP 10

PROPITHECUS GROUP 10: Group composition consisted of one adult male (Sam), one adult female (Alice), and one juvenile female (Olive). The juvenile was approximately one year old at the time of this research.
Adult male fitted with radio collar. Female fitted with pink collar.
Female 6.7 kg, body length 47.5 cm, tail length 50 cm
Male 5.6 kg, body length 43 cm, tail length 45 cm

Overall size of substrate: A 6.9%, B 45.9%, C 41.5%, D 5.5%
Overall height of substrate: A 13.7%, B 10.3%, C 7.9%, D 3.8%, E 20.7%, F 22.0%, G 16.9%, Ground 0.3%, H 3.9%, I 0.5%
Overall quadrant: Quad1 5.2%, Quad2 2.2%, Quad3 3.2%, Quad4 6.2%, Quad5 17.1%, Quad6 37.7%, Quad7 23.5%, Quad8 0.1%, Rav Palm5 0.1%, Dead Tree 0.1%, Fallen Branch 0.1%, Fallen tree 0.1%, Liana 0.1%, Liana Tangle 0.1%
Overall orientation: A 26.0%, B 48.5%, C 25.5%
Total activity budget: Eat Fruit 3.6%, Eat Flowers 8.5%, Eat Leaves 5.6%, Eat Young Leaves 5.6%, Groom Other 2.5%, Groom-self 8.5%, Move 11.7%, Mark 1.1%, Rest 44.8%
Total tree height: A 0.7%, B 5.4%, C 5.0%, D 6.2%, E 8.8%, F 37.8%, G 25.7%, Ground 0.1%, H 9.3%, I 1.1%

The other group of sifaka that was part of the all day follows inhabited space in the southern portion of the reserve closer to the invasive guava and areas of non-primary forest. Olive was born in June 2008 and was doing well traveling, foraging, and resting cohesively with Sam and Alice. This group was much more cohesive as a unit, traveling, resting, and feeding together, in comparison to sifaka group 1. The male was fitted with the radio collar and so became the focal animal of much of the recorded behavioral observations. Out of the overall total activity budget for sifaka group 10 they spent 45% resting, 32% eating, and 10% moving (Figure 6.5).

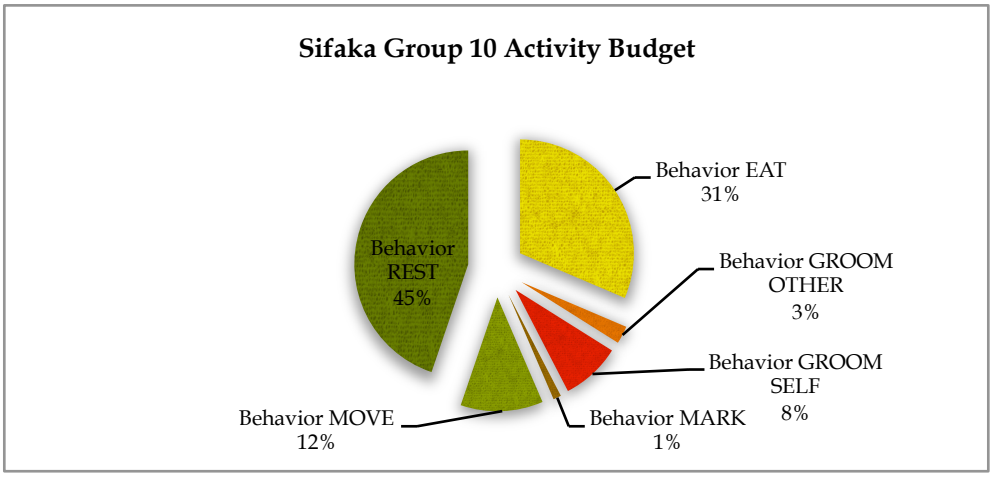


Figure 6.5 Sifaka Group 10 activity budget

FEEDING BEHAVIORS FOR SIFAKA GROUP 10

Types of foods consumed by sifaka group 10

Out of the total amount of time spent engaged in feeding behavior, the sifaka spent the most time feeding on leaves (43.8%) and flowers (26.9%) (Table 6.57). In comparison to sifaka group 1, the sifaka in group 10 had less variety in the foods they consumed. But, they consumed a higher proportion of each of the foods presented in Table 6.57 perhaps to compensate for this lack of variety and to ensure complete nutrition.

Table 6.57 Foods consumed by sifaka group 10

Food (N=475)	Total Count	Percentage
Fruit	54	11.4%
Flowers	128	26.9%
Mature Leaves	208	43.8%
Young Leaves	85	17.9%

Postures used for the consumption of different foods by sifaka group 10

Sifaka in group 10 displayed a variety of different postures for the consumption of different food items (Table 6.55). The most common posture for eating was a vertical cling (29.7%) followed by a sit (25.4%) (Table 6.58). The frequent use of a vertical cling posture for feeding behavior may be a reflection of their more active lifestyle in comparison to the sifaka in group 1. Sifaka in group

10 were very mobile and often were still chewing the food or holding the food item from the previous tree as they moved to the next substrate

Table 6.58 Posture used for food consumption by sifaka group 10

Posture (N=508)	Total Count	Percentage	Food eaten in posture	Percentage
Recline	21	10.6%	EF, EFL, EL, EYL	4.8%, 61.9%, 23.8%, 1.3%
Sit Extend	90	17.7%	EF, EFL, EL, EYL	6.7%, 35.6%, 50%, 7.8%
Sit	129	25.4%	EF, EFL, EL, EYL	17.1%, 15.5%, 55.8%, 11.6%
Stand	1	0.2%	EYL	100%
Suspend	83	16.3%	EF, EFL, EL, EYL	2.4%, 45.8%, 34.9%, 16.9%
Vertical Cling	151	29.7%	EF, EFL, EL, EYL	15.2%, 16.6%, 37.7%, 30.5%

Size of substrate used by sifaka group 10 while feeding

Small sized substrates (1-5 cm dbh) were the most common overall supportive material the sifaka used in their daily activities. This use of small substrates is also a common sized substrate (45.9%) along with medium substrates (41.5%) used in their feeding behavior (Table 6.59).

Table 6.59 Size of substrate used for food consumption by sifaka group 10

Size of Substrate Used in Feeding	Count	Percentage of Use
Very Small (<1cm)	105	6.9%
Small (1-5 cm)	695	45.9%
Medium (6-10cm)	628	41.5%
Large (11-15 cm)	84	5.6%

Height of substrate used by sifaka group 10 while feeding

The sifaka in group 10 used a wide range of heights for feeding behavior (Table 6.60). The highest percentage of time was focused on feeding at 11 meters. However, the sifaka also spent significant amounts of time feeding at 1 to 3 and 7 to 10 meters. The sifaka focused on young leaves (53.7%) and mature leaves (40.6%) at lower heights and fruits (29.2%) and flowers (29.7%) at taller heights.

Table 6.60 Height of substrate used for food consumption by sifaka group 10

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	62	13.1%
B (2-3 m)	71	14.9%
C (4-5 m)	21	4.4%
D (6 m)	31	6.5%
E (7-8 m)	63	13.2%
F (9-10 m)	84	17.7%
G 11 (m)	101	21.3%
H (12-13 m)	36	7.6%
I (14-15 m)	6	1.3%

Orientation of substrate used by sifaka group 10 while feeding

The sifaka in group 10 frequently used oblique substrates for most feeding behaviors (52.0%) (Table 6.61). When feeding on young leaves from flimsy trees at lower heights, the sifaka vertically clung to adjacent small or medium substrates to support their body weight while feeding. As such, the sifaka focused more so on vertical substrates when feeding on young leaves (Table 6.61)

Table 6.61 Orientation of substrate used for food consumption by sifaka group 10

Food	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%
Fruit	18	33.3%	27	50.0%	9	16.7%
Mature Leaves	65	31.3%	101	48.6%	42	20.2%
Flowers	36	28.1%	79	61.7%	13	10.2%
Young leaves	1	1.2%	40	47.1%	44	51.8%

Use of different tree quadrants while feeding by sifaka group 10

The sifaka spent a majority of their feeding time in quadrants 6 (25.5%) and 7 (20.0%), although the sifaka used a variety of different quadrants including lianas and liana tangles (Table 5.62). The sifaka mainly consumed fruit and flowers in the peripheral quadrants of the tree. The sifaka consumed a higher percentage of leaves in quadrant 5 as well as quadrant 6. Quadrants 4

and 7 were used more commonly for feeding on young leaves. The sifaka ate young leaves from smaller trees in the lower canopy. They either sat in the tree canopy such that their body consumed the entire space (quadrant 4) or they would vertical-cling to quadrant 7 of the adjacent tree, in order to support their body weight, as they fed on the smaller treelets.

Table 6.62 Quadrants used for food consumption by sifaka group 10

Quadrant	Quad 1 (N=16)	Quad 2 (N=22)	Quad 3 (N=39)	Quad 4 (N=65)	Quad 5 (N=71)	Quad 6 (N=110)	Quad 7 (N=85)	Rav Palm5 (N=2)	Liana (N=19)	Liana Tangle (N=2)
Fruit	3	1	12	5	13	14	6	0	0	0
Flowers	1	5	10	13	54	30	13	0	0	2
Leaves	12	15	17	18	47	53	37	2	7	0
Young Leaves	0	2	0	29	0	13	29	0	12	0

Foods consumed in different levels of canopy/vegetation connectivity by sifaka group 10

Sifaka in group 10 engaged in feeding behavior more frequently in connected canopy (Table 6.63). The types of foods eaten in this connected layer consisted of all the food types with the least amount of focus on fruits (4.1%). In comparison to the other food types, flowers (75.5%) were eaten the most in the connected/small-gapped canopy and leaves more so in the small (47.1%) and medium (64.7%) gapped canopy. No foods were eaten in areas with small/medium gaps. Out of a comparison of all the levels of connectivity, the sifaka consumed fruit (75.9%) frequently in areas of small gaps and flowers (43.4%), leaves (58.7%), and young leaves (94.1%) within connected canopy areas.

Table 6.63 Canopy distances and different foods consumed by sifaka group 10

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Eat fruit	11 (4.1%)	0 (0%)	41 (34.5%)	0 (0%)	2 (5.9%)
Eat flowers	56 (20.8%)	40 (75.5%)	22 (18.5%)	0 (0%)	10 (29.4%)
Eat mature leaves	122 (45.4%)	8 (15.1%)	56 (47.1%)	0 (0%)	22 (64.7%)
Eat young leaves	80 (29.7%)	5 (9.4%)	0 (0%)	0 (0%)	0 (0%)
Total	269	53	119	0	34

LOCOMOTION BY SIFAKA GROUP 10

Locomotor modes used by sifaka group 10

The sifaka individuals in group 10 spent a higher percentage of time resting compared to moving and eating behaviors. However, the duration of time for each resting bout for this sifaka group was much shorter. At most, they might rest for half an hour during the day and then they were on the move again. This sifaka group rested in short bursts between vertical clings and leaps as they moved through this forest. Sifaka group 10 was the fastest and most active group out of all the lemur groups followed in this research. Movement through the forest consisted of varying distances with a focus on one and two meter leaps (Table 6.64).

Table 6.64 Locomotor modes used by sifaka group 10

Locomotor Modes (N=177)	Total Count	Percentage
Climb	16	9.0%
L<1	21	11.9%
L1	65	36.7%
L2	52	29.4%
L3	16	9.0%
L4	4	2.3%
Vertical Bound	3	1.7%

Size of substrate used for locomotion by sifaka group 10

The size of substrate affects movement (K-S, D_{MAX}=0.22, p<0.01). Sifaka in group 10 were capable of using a variety of different sized substrates for movement (Table 6.65) including the ground. The sifaka frequently used small (47.5%) and medium (43.5%) substrates for movement.

Table 6.65 Different sized substrates for movement by sifaka group 10

Size of Substrate	Very small	Small	Medium	Large
Move	6	84	77	10

If the correlated behavior "move" is divided further into the various locomotor modes, the main movement by sifaka group 10 was onto small and medium substrates by leaping one and two meters (Table 6.66). The sifaka rarely used very small or large substrates for movement. Additionally, no consistent pattern emerged of the use of these very small or large substrates. For example, the sifaka did not use very small substrates for short leaps and large substrates for long leaps, rather the sifaka used whatever was available to reach their destination.

Table 6.66 Locomotor modes on varying sized substrates by sifaka group 10

Size of Substrate	Ground	Very Small	Small	Medium	Large
Climb	0	1	6	8	1
L<1	3	0	12	9	0
L1	1	4	34	24	2
L2	0	1	24	24	3
L3	0	0	7	8	1
L4	0	0	1	2	1
Vertical Bound	0	0	0	2	1

Heights used by sifaka group 10 for locomotion

Height of substrate affects sifaka movement (K-S, D_{MAX}=0.33, p<0.01). The main height used for moving by sifaka group 10 was very low at a height of one meter (43.0%). The heights between two and five meters were also used (Table 6.67). The sifaka focused on using one and two meter

leaps at a height of one meter although a range of distances was implemented. Overall, the sifaka moved much lower in the canopy with the frequency of movement at taller heights dwindling past 11 meters. The sifaka were observed to use the ground or substrates lying on the ground (e.g. fallen tree trunk) on several occasions as they moved through the forest.

Table 6.67 Different heights used for movement by sifaka group 10

Height of substrate	A	B	C	D	E	F	G	Ground	H	I
Climb	2	1	3	1	2	2	3	0	1	1
L<1	12	4	0	0	1	1	1	3	1	0
L1	29	10	6	4	8	5	1	1	0	0
L2	20	8	10	4	4	3	0	0	3	0
L3	1	4	3	0	1	3	2	0	2	0
L4	1	0	2	0	1	0	0	0	0	0
Vertical Bound	0	1	0	0	1	0	0	0	0	0

Substrate orientations used for different locomotor modes by sifaka group 10

Orientation of substrate influences movement (χ^2=175, df=2, p<0.001). Sifaka in group 10 used vertical substrates for moving (78.9%), and to a lesser extent oblique (18.9%) and horizontal (2.2%) (Table 6.68).

Table 6.68 Locomotor modes used on varying oriented substrates by sifaka group 10

Orientation	Horizontal	Oblique	Vertical
Climb	0	5	14
L<1	1	5	15
L1	2	11	52
L2	1	7	44
L3	0	4	12
L4	0	1	3
Vertical Bound	0	1	2
Total	4	34	142

Quadrant use for movement by sifaka group 10

Movement is influenced by tree quadrant (χ^2=342, df=6, p<0.001). When moving, sifaka in group 10 used all of the quadrants (except quadrant 3), with the highest frequency of use in

quadrant 7 (67.0%) (Table 6.69). Sifaka also used other quadrants in the environment beyond just the tree canopy and trunk, including ravinala palms, fallen branches, the ground, and lianas. Climbing and ≤1 meter leaps commonly occurred within the canopy crown for within-substrate movement and all distance leaps occurred onto quadrant 6 and 7 for between tree movements.

Table 6.69 Movement in varying quadrants by sifaka group 10

Quadrant	1	2	3	4	5	6	7	8	Rav Palm 5	Fallen Branch	Liana
Move	2	2	0	2	3	20	134	4	4	1	8

Canopy/vegetation connectivity and locomotor modes by sifaka group 10

Canopy/vegetation connectivity affects sifaka movement (K-S, D_{MAX}=0.46, p<0.01). Sifaka in group 10 primarily moved through areas with connected canopy/vegetation (Table 6.70) by one and two meter leaps (Table 6.71). The sifaka used a wide range of areas that consisted of varying degrees of connectivity from connected canopy/vegetation to areas that have medium/large gaps in the forest space. The connectivity of the canopy/vegetation did not affect locomotor modes (χ^2=8.06, df=3, p>0.001). Regardless of the level of connectivity the sifaka still moved through these areas with one and two meter leaps (Table 6.71).

Table 6.70 Different levels of canopy connectedness used for movement by sifaka group 10

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium	Medium/Large
MOVE	134	6	29	2	5	1

Table 6.71 Levels of canopy connectedness and locomotor modes by sifaka group 10

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium	Medium/Large
Climb	7	1	6	0	2	0
L<1	14	2	4	0	1	0
L1	55	1	8	0	1	0
L2	45	0	6	0	1	0
L3	9	0	4	2	0	1
L4	2	1	1	0	0	0
Vertical Bound	2	1	0	0	0	0

Overall, the sifaka used between-substrate movement a higher percentage of time (87.6%) than within-substrate movement (12.4%). The between-substrate movement through the forest consisted of varying distance leaps whereas the within-substrate movement consisted of climbing, short leaps, and vertical bounding (Figure 6.6).

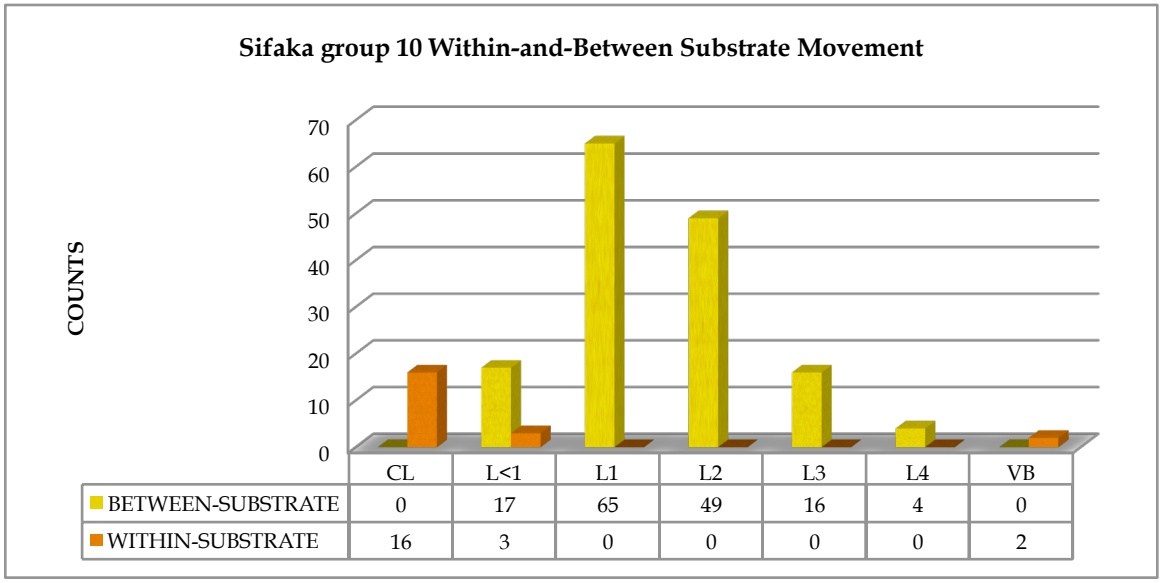


Figure 6.6 Sifaka group 10 within-and-between group movement

RESTING BEHAVIORS BY SIFAKA GROUP 10

Postures used for resting by sifaka group 10

The sifaka in group 10 rested in three main postures, including a sit-extend (37.3%), sit (40.6%), and vertical cling (22.0%) (Table 6.72). For more extended resting periods the sifaka used sit postures, whereas vertical-clinging postures were usually used for brief rest periods between leaps.

Table 6.72 Different postures used while resting by sifaka group 10

Postural modes for Rest (N=677)	Total Count	Percentage
Sit-Extend	253	37.3%
Sit	275	40.6%
Vertical Cling	149	22.0%

Size of substrate used for resting by sifaka group 10

Sifaka resting behaviors are influenced by the size of substrate (K-S, D_{MAX}=0.23, $p<0.01$). The sifaka commonly rested on small (45.5%) and medium (48.0%) substrates, but rarely rested on very small or large substrates (Table 6.73).

Table 6.73 Different sized substrates used for resting by sifaka group 10

Size of Substrate Resting	Total Count	Percentage
Very Small (<1 cm)	8	1.2%
Small (1-5 cm)	308	45.5%
Medium (6-10 cm)	325	48.0%
Large (11-15 cm)	36	5.3%

Size of substrate used for different resting postural modes by sifaka group 10

When resting in a sit or vertical-cling posture the sifaka used a higher percentage of medium substrates (Table 6.74). Whereas when the sifaka were resting in a sit-extend posture, smaller sized substrates were used (Table 6.74). Occasionally the sifaka were observed to rest in a sit-extend posture on very small substrates.

Table 6.74 Size of substrate used for different resting postures by sifaka group 10

Size of Substrate	Very Small	%	Small	%	Medium	%	Large	%
Sit-extend	7	2.8%	174	68.8%	61	24.1%	11	4.3%
Sit	0	0	87	31.6%	166	60.3%	22	8%
Vertical cling	1	0.7%	47	31.5%	98	65.8%	3	2.0%

Substrate orientation used for resting by sifaka group 10

Sifaka resting behaviors are influenced by orientation of substrate (χ^2=117.2, df=2, p<0.001). While resting, sifaka group 10 spent a higher percentage of time on oblique substrates (51.8%) (Table 6.75).

Table 6.75 Different orientations used for resting behaviors by sifaka group 10

Horizontal Count	%	Oblique Count	%	Vertical Count	%
202	29.8%	351	51.8%	124	18.3%

Height of substrate and resting behavior by sifaka group 10

Sifaka resting behaviors are influenced by substrate height (K-S, D_{MAX}=0.21, p<0.01). The sifaka in group 10 rested at a variety of heights (1 to 15 meters), but a higher percentage occurred at the heights between 7 and 11 meters (68.2%) meters (Table 6.76).

Table 6.76 Different heights used for resting by sifaka group 10

Height of Substrate	A	B	C	D	E	F	G	H	I
Rest	75	53	56	15	166	173	123	15	I

Quadrant use and resting behavior by sifaka group 10

Sifaka have a preference for certain quadrants for resting (χ^2=1030, df=7, p<0.001). Sifaka in group 10 rested in an eclectic range of quadrants, including ravinala palms, dead trees, lianas, and liana tangles (Table 6.77). However, more than half of the resting time occurred in quadrant 6 (53.5%) (Table 6.77).

Table 6.77 Different quadrants used for resting by sifaka group 10

Quadrant	1	2	3	4	5	6	7	Rav Palm5	Dead tree	Liana	Liana Tangle
Rest	50	8	10	20	96	334	123	1	2	10	20

Canopy/vegetation connectivity and resting behaviors by sifaka group 10

Canopy/vegetation connectedness affects sifaka resting behavior (K-S, D_{MAX}=0.24, p<0.01). The sifaka in group 10 rested primarily in areas of connected (48.7%) and small-gapped (28.2%) canopy/vegetation (Table 6.78).

Table 6.78 Levels of connectedness in canopy/vegetation used for resting by sifaka group 10

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium	Medium/Large
Rest	330	64	191	2	89	1

SIFAKA GROUP 10 SUBSTRATE COMBINATIONS AND NEAREST NEIGHBOR

Substrate Combinations

Orientation of substrate and quadrant use by sifaka group 10

The sifaka frequently occupied horizontal substrates when utilizing quadrants 1 (87.2%) and 5 (61.4%). While in quadrant 6 (81.2%) the emphasis was on oblique substrates and quadrant 7 was vertical substrates (95.8%) (Table 6.79). The quadrants outside of the canopy and trunk were in used a variety of combinations with differently oriented substrates.

Table 6.79 Orientation and quadrant used by sifaka group 10

Quadrant	Horizontal	Oblique	Vertical
1	68	9	1
2	12	18	3
3	16	33	0
4	28	60	6
5	159	99	1
6	95	463	12
7	1	14	341
8	1	0	0
Rav Palm 5	0	0	7
Dead Tree	0	2	0
Fallen Branch	1	1	0
Fallen Tree	1	1	0
Liana	5	17	15
Liana Tangle	6	16	0

Height of substrate and quadrant use by sifaka group 10

Sifaka tended to use quadrant 7, lianas, dead trees, and fallen branches (or other substrates cluttering the forest floor) when they occupied lower heights in the forest (Table 6.80). A variety of different height and quadrant combinations were used by the sifaka in group 10. Some interesting patterns included an emphasis of quadrant 1 at a height of 11 meters and quadrants 6 and 7 at the height of 9 to 11 meters. Lianas were used at a variety of different heights. The sifaka used lianas that were their own entity or lianas attached to trees or other vegetation.

Table 6.80 Height of substrate and quadrant used by sifaka group 10

Height of Substrate	Quad 1	Quad 2	Quad 3	Quad 4	Quad 5	Quad 6	Quad 7	Liana	Dead Tree	Fallen Branch	Fallen tree	Rav Palm5	Liana Tangle
A	0	0	0	0	0	0	4	3	2	1	1	0	0
B	1	0	0	25	0	14	29	9	0	0	0	0	3
C	0	0	0	0	0	27	32	1	0	1	1	2	11
D	0	0	0	1	4	53	27	4	0	0	0	4	0
E	0	7	9	8	1	37	64	1	0	0	0	0	6
F	1	2	31	20	145	216	147	7	0	0	0	1	2
G	75	5	6	16	36	197	45	9	0	0	0	0	0
H	1	19	1	24	67	19	6	3	0	0	0	0	0
I	0	0	2	0	6	7	1	0	0	0	0	0	0

Total tree height and height of substrate used by sifaka group 10

The sifaka in group 10 used a variety of different height of substrate and height of tree combinations, suggesting the total tree height does not influence the height used by the sifaka (Table 6.81). Similar to sifaka group 1, sifaka group 10 often chose to engage in behaviors at a height right below the total height of the tree or the actual total height of the tree. The sifaka sat in trees that had tall slender trunks and narrow canopy widths such that the sifaka's body monopolized the entire volume of the tree's foliage.

Table 6.81 Height of substrate and total height of tree used by sifaka group 10

Height of tree	A	B	C	D	E	F	G	H	I
Height of Substrate									
A	11	45	32	20	34	57	8	0	0
B	0	36	39	29	19	31	2	0	0
C	0	0	4	39	23	46	7	0	0
D	0	0	0	5	24	25	4	0	0
E	0	0	0	0	30	267	16	0	0
F	0	0	0	0	1	146	184	2	0
G	0	0	0	0	0	0	168	86	1
H	0	0	0	0	0	0	0	52	7
I	0	0	0	0	0	0	0	0	8

Keystone Structures

The sifaka frequently used cluttered space that consisted of the expansive growth of liana, bamboo, and vine tangles. The vegetation the sifaka utilized was often connected. This group also had the capacity to use areas of taller canopy with more open space.

The sifaka in this group demonstrated a heightened frequency of use of certain substrates in their environment. These keystone elements included a liana swing the sifaka used to cross a large open gap in the forest canopy. This gap was due to sporadic canopy combined with an abrupt steep decline in the landscape. The sifaka repeatedly used this liana swing to move across this open area. The sifaka also repeatedly used select large (54 cm dbh) fallen trees that laid on steep inclines for movement. The landscape was steep in these areas. This landscape feature combined with the thick understory vegetation created a difficult situation to maneuver through, making bounding up a fallen tree much easier movement option. Sifaka in group 10 were repetitive in their paths and use of substrates like fallen trees or lianas. Some other important keystone structures are presented in Table 6.82.

Table 6.82 Keystone structures for sifaka group 10

Malagasy tree	Dbh (cm)	Height (m)	Activity	GPS
Mampay	8	6.9	Feeding leaves and seeds	(0309095, 8018300)
Liana swing	14	11	Moving	(0309097, 8018219)
Hazoambovahy	39	10.3	Feeding leaves	(0309033, 8018406)
Fomotrorana	52	9.4	Feeding fruit	(0309088, 8018181)
Hazoambo	40	10.6	Feeding fruit	(0309175, 8017840)
Lianna on Mampay	5	6.3	Feeding leaves	(0309361, 8017691)
Dongavelona	32	10.8	Feeding flowers	(0309434, 8017645)

SIFAKA GROUP 10 AND NEAREST NEIGHBOR

Identity of nearest neighbor

The most common nearest neighbor to the focal male was the juvenile (61.4%). Sifaka group 10 was a very cohesive unit that traveled, foraged, and rested together (Table 6.83).

Table 6.83 Nearest neighbors to focal sifaka male in group 10

Female	Female/Juvenile	Juvenile	>20 m
300	228	840	40

Distance of nearest neighbor

Less than one meter was the most common distance from the focal male to the juvenile of female (Table 6.84). A nearest neighbor was never more than six meters away from the focal animal.

Table 6.84 Distances of nearest neighbors to focal sifaka male group 10

Distances (m)	0	1	2	3	4	5	6
Female	128	51	56	55	8	2	0
Female/Juvenile	80	33	22	27	20	46	0
Juvenile	513	127	134	106	21	13	3
Total	712	211	212	188	49	61	3

Sifaka Group 10 Summary Statement

Certain microhabitat features influenced sifaka group 10 movement, feeding, and resting behaviors. These paragraphs highlight those substrates the sifaka utilized at a higher frequency than others, but as noted in the preceding sections, sifaka in group 10 were capable of utilizing a wide range of different heights and substrates for resting, eating, and moving. Sifaka in group 10 frequently used small (45.9%) and medium (41.5%) substrates for resting, feeding, and moving behaviors. Additionally, the sifaka used a height of 7 to 10 meters in quadrant 6 on oblique substrates in 10 meter tall trees. The sifaka spent a majority of their activity budget resting. This higher resting percentage is a reflection of short bursts of rest in between vertical-clinging-and-

leaping bouts. Sifaka in group 10 rarely rested for extended periods of time. Some days the sifaka moved all day long and hardly took a moment to rest.

This group rested, moved and fed in areas with abundant underbrush, tree falls ensconced in bamboo and mazomboty, and dead thickets of vines. The landscape was undulant and often consisted of steep slopes of scree and large boulders, creating a staggered and choppy canopy with a dense three meter canopy layer with abundant 1-5 cm dbh trees. During each all day follow of sifaka group 10 the trees utilized for resting, moving, and feeding were flagged and identified when possible. Please note this is not an exhaustive list especially given the rapid speed and agility sifaka travel with it was difficult to mark down every tree. This list is included in the appendix. The overall main five trees used were azinina (N=7), mampay (N=7), tavolo fotsy (N=7), liana (N=6), and rara (N=6). Sifaka used keystone structures in their environment. This included important feeding trees but also important substrates for movement. Sifaka in group 10 were repetitive in their paths and use of substrates like fallen trees or specific lianas.

Out of the total amount of time spent feeding, sifaka in group 10 spent the most time eating leaves (43.8%) and flowers (26.9%). Sifaka in group 10 were not observed to have the same variety of foods in their diet as that of the sifaka in group 1. The sifaka in group 10 spent a higher percentage of time consuming flowers and fruits perhaps to compensate for this smaller array of foods. The differences in foods consumed by the two sifaka groups could be due to a lack of availability of certain foods in the southern portion of the reserve, the active choice by the sifaka to consume those foods, or were simply not observed to be consumed by the observer. The most common postures for feeding behaviors were vertical clinging and sitting. This sifaka group also engaged in suspensory postures for feeding behaviors (more so than group 1). The common use of the vertical cling posture for feeding may echo their propensity to keep moving. The sifaka in group 10 were were still chewing and/or holding the food item from the previous tree as they moved to the next tree. The sifaka used very small and small oblique substrates for a majority of their feeding

behaviors at a height of 11 meters in quadrant 6. Feeding behaviors also commonly occurred in areas of connected canopy/vegetation, although the sifaka used a broad range of different levels of connectivity including open areas with medium gaps.

The sifaka moved through connected canopy/vegetation using a range of leaping distances, but focused on one and two meter leaps onto small and medium vertical substrates at a lower height of one meter. The sifaka used a wide range of quadrants to move, including the ground, ravinala palms, fallen branches, and lianas, but most of the focus was on quadrant 7. A majority of the sifaka movement was between-substrate movement rather than within-substrate movement.

For extensive rest periods, the sifaka assumed a sit or sit-extend posture on small oblique substrates whereas vertical cling resting postures occurred on medium vertical substrates. The sifaka occupied heights between 7 and 10 meters for rest mainly in quadrant 6, although a majority of rest also occurred in quadrant 7. Most of the resting occurred in areas of connected or small-gapped canopy/vegetation.

Sifaka group 10 traveled, foraged, and rested together more frequently as a unit than apart. Less than one meter was the most common distance from the focal male to the juvenile or the female. A nearest neighbor was never more than six meters away from the focal animal. The nearest neighbor was often the juvenile in these situations. Occasionally the male or female traveled more than 20 meters ahead or behind the others. The juvenile was just as likely to partner up with the male or the female if the group split in this manner. The group would split for brief periods of time but would soon reconvene.

Sifaka group 10 was highly flexible in their ability to utilize a wide spectrum of different substrates, orientations, and heights for resting, feeding, and moving behaviors. The sifaka appear to have a heightened preference for certain substrates but were also quick to make adjustments and use other forest elements.

Subsection 6.4
INDRI GROUP 40

INDRI GROUP 40: Group composition consists of one adult solitary female, Lenore.
Female 7.5 kg, body length 52 cm, tail length 5cm

Summary of substrate use and total activity budget for Indri Group 40
Overall size of substrate: A 2.3%, B 28.7%, C 46.0%, D 23.0%
Overall height of substrate: A 0.5%, B 6.1%, C 13.6%, D 12.6%, E 12.3%, F 22.8%, G 10.5%, H 18.9%, I 2.8%
Overall quadrant: Quad1 1.3%, Quad2 5.5%, Quad3 5.6%, Quad4 16.7%, Quad5 14.6%, Quad6 37.0%, Quad7 16.9%, Liana 1.6%, Knot 0.7%
Overall orientation: A 39.1%, B 44.9%, C 16.0%
Total activity budget: Eat fruit 0.1%, Eat flowers 2.1%, Eat leaves 27.9%, Eat leaf base 0.8%, Eat young leaves 9.3%, Groom-self 1.6%, Kiss 0.4%, Move 6.4%, Mark 0.1%, Rest 51.2%
Total tree height: B 0.2%, C 1.0%, D 5.3%, E 10.3%, F 24.9%, Fallen tree 0.5%, G 22.7%, H 29.4%, I 5.8%

Lenore spent almost equal proportions of her time eating and resting with a much smaller percentage of her time moving (Figure 6.6). Despite her single status, Lenore still sang her portion of the duet to announce her territory. Also interesting about Lenore is the amount of time she dedicated to feeding. She often spent hours in a single tree eating leaf after leaf.

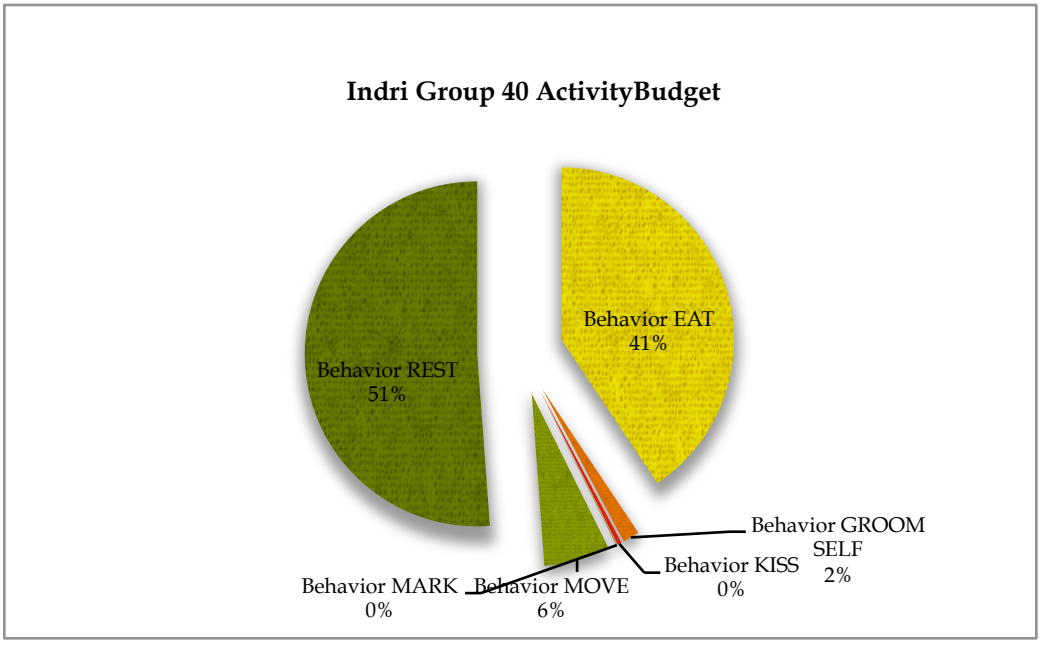


Figure 6.7 Indri group 40 activity budget.

FEEDING BEHAVIORS BY INDRI GROUP 40

Types of foods consumed by indri group 40

Out of the total amount of time spent engaged in feeding behavior, Lenore spent the most time feeding on mature leaves (69.3%) and young leaves (23.1%) (Table 6.85).

Table 6.85 Foods consumed by indri group 40

Food (N=619)	Total Count	Percentage
Fruit	2	0.3%
Flowers	33	5.3%
Mature Leaves	429	69.3%
Leaf Base	12	1.9%
Young Leaves	143	23.1%

Postures used for the consumption of different foods by indri group 40

Lenore displayed a variety of different postures for the consumption of different food items (Table 6.86). The most common posture for all foods was a sit (47.0%) followed by sit-extend (22.9%) and vertical cling (18.3%). While in a vertical cling posture, Lenore focused on eating leaves and young leaves. This posture generally occurred when Lenore fed from trees that were not strong enough to bear her weight. She held onto an adjacent sturdier tree while consuming the foliage from the weaker treelet or shrub. This type of feeding behavior often occurred at lower heights in the canopy.

Table 6.86 Postures used for food consumption by indri group 40

Posture (N=619)	Total Count	Percentage	Food eaten in posture	Percentage
Recline	61	10%	EFL, EL, ELB[16], EYL	1.6%, 73.8%, 3.3%, 21.3%
Sit Extend	142	22.9%	EFL, EL, EYL	2.1%, 75.4%, 22.5%
Sit	291	47.0%	EF, EFL, EL, ELB, EYL	0.7%, 4.7%, 73.5%, 3.4%, 12.4%
Suspend	12	1.9%	EL, EYL	16.7%, 83.3%
Vertical Cling	113	18.3%	EL, EYL	54.0%, 46%

[16] ELB=eat tree bark

Size of substrate used by indri group 40 while feeding

Lenore used medium sized substrates more than half of the time for feeding behavior (Table 6.87). She also used small substrates (34.6%) and to a lesser extent, large substrates (12.2%).

Table 6.87 Size of substrate used for food consumption by indri group 40

Size of Substrate Used in Feeding	Count	Percentage of Use
Very Small (<1cm)	11	1.8%
Small (1-5 cm)	213	34.6%
Medium (6-10cm)	316	51.4%
Large (11-15 cm)	75	12.2%

Height of substrate used by indri group 40 while feeding

Lenore used a wide range of heights for feeding behaviors with more frequent use of the heights of 9 to 10 meters, 12 to 13 meters, and the lower heights of 6 to 8 meters (Table 6.88). The main foods consumed at the taller heights were mainly mature leaves, although young leaves were also equally consumed at lower heights. The majority of flower consumption occurred between the heights of 7 and 10 meters.

Table 6.88 Heights used for food consumption by indri group 40

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	1	0.2%
B (2-3 m)	46	7.3%
C (4-5 m)	55	8.7%
D (6 m)	91	14.5%
E (7-8 m)	99	15.7%
F (9-10 m)	132	21.0%
G 11 (m)	57	9.1%
H (12-13 m)	131	20.8%
I (14-15 m)	17	2.7%
Total	629	100%

Orientation of substrate used by indri group 40 while feeding

Lenore commonly used horizontal substrates for feeding behaviors. Specifically, more than half of the leaves Lenore consumed were on horizontal branches (Table 6.89). A majority of young

leaves were also consumed on horizontal substrates Lenore used oblique substrates for more than half of her flower consumption. The only foods consumed on vertical substrates were leaves (53.6%) and young leaves (46.4%).

Table 6.89 Orientation of substrate used for food consumption by indri group 40

Food (N=619)	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%	Total
Eat fruit	2	100%	0	0%	0	0%	2
Eat flowers	6	18.2%	27	81.8%	0	0%	33
Eat mature leaves	240	55.9%	144	33.6%	45	10.5%	429
Eat leaf base	0	0%	12	100%	0	0%	12
Eat young leaves	62	43.4%	42	29.4%	39	27.3%	143
TOTAL	310		225		84		619

Use of different tree quadrants while feeding by indri group 40

The most frequented canopy/trunk quadrant for feeding behaviors was quadrant 4 (31.2%) while the least was quadrant 1 (2.4%). Lenore used the greatest variety of quadrants for the consumption of leaves (Table 6.90), including the use of lianas and tree knots. Lenore used knots on the sides of oblique or vertical tree trunks as a support while feeding. She often let her feet dangle relying solely on the support of the knot. She tended to hold on with her feet if she was sitting on a more vertically oriented substrate.

Table 6.90 Quadrant used for food consumption by indri group 40

Food	Quad 1	Quad 2	Quad 3	Quad 4	Quad 5	Quad 6	Quad 7	Liana	Tree Knot
Fruit	0	0	0	0	2	0	0	0	0
Flowers	0	0	0	14	4	15	0	0	0
Mature Leaves	15	49	17	121	108	61	51	4	3
Leaf base	0	0	0	12	0	0	0	0	0
Young leaves	0	0	34	46	0	27	28		8
Total	15	49	51	193	114	103	79	4	11

Foods consumed in different levels of canopy/vegetation connectivity y indri group 40

Lenore mainly foraged in areas with connected canopy/vegetation (44.6%) (Table 6.91), especially her consumption of mature and young leaves. Although leaves, a major dietary food item, were consumed in parts of the forest with all the varying levels of connectivity.

Table 6.91 Canopy/vegetation distances and foods consumed by indri group 40

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium
Eat fruit	2	0	0	0
Eat flowers	19	14	0	0
Eat mature leaves	149	94	61	125
Eat leaf base	12	0	0	0
Eat young leaves	94	49	0	0
Total	276	157	61	125

LOCOMOTION BY INDRI GROUP 40

Locomotor modes by indri group 40

Lenore spent more time resting and eating than she did moving. The movement throughout the forest was accomplished through vertical leaps of varying distances from one up to four meters (Table 6.92). The majority of the leaps were in one (39.8%) or two (32.7%) meter increments.

Table 6.92 Locomotor modes used by indri group 40

Locomotor mode (N=98)	Total Count	Percentage
Climb	6	6.1%
L1	39	39.8%
L2	32	32.7%
L3	9	9.2%
L4	8	8.2%
Vertical Bound	4	4.1%
TOTAL	98	100%

Size of substrate used for locomotion by indri group 40

Size of substrate does not affect movement for Lenore (K-S, D_{MAX}=0.03, p>0.05). Lenore used small, medium, and large substrates relatively equally for movement throughout the forest (Table 6.93).

Table 6.93 Different sized substrates for movement by indri group 40

Size of Substrate	Small	Medium	Large
Move (N=98)	31 (31.6%)	37 (37.8%)	30 (30.6%)

Most of Lenore's one meter leaps occurred on small (48.7%) and medium (38.5%) substrates, whereas two meter leaps were more commonly made onto medium (43.8%) and large (34.4%) with less focus on small substrates (21.9%) (Table 6.94). Despite the small sample size, Lenore frequently used larger sized substrates for longer distance leaps. Yet, this pattern is broken with Lenore's four meter leaps onto small substrates, indicating flexibility in her use of different sized substrates that seems contingent upon what is immediately available to move in the direction of her destination.

Table 6.94 Different locomotor modes on varying sized substrates by indri group 40

Size of Substrate	Small	Medium	Large	Total
Climb	2	1	3	6
L1	19	15	5	39
L2	7	14	11	32
L3	1	3	5	9
L4	2	2	4	8
Vertical Bound	0	2	2	4
Total	31	37	30	98

Heights used by indri group 40 for locomotion

The height of substrate does not affect movement for Lenore (K-S, D_{MAX}=0.13, p>0.05). Lenore used a wide range of different heights, 4 to 10 meters, for movement (Table 6.95). The main type of locomotion at these heights was by one and two meter leaps (Table 6.96). The longer distance leaps of 4 meters frequently occurred at taller heights above 10 meters.

Table 6.95 Different heights used for movement by indri group 40

Height of Substrate	A	B	C	D	E	F	G	H
Move	3	3	21	17	16	22	9	7

Table 6.96 Height of substrate and locomotor mode by indri group 40

Height of substrate	A	B	C	D	E	F	G	H
Climb	0	0	2	1	0	0	3	0
L1	3	1	7	11	8	5	0	4
L2	0	1	7	5	6	12	0	1
L3	0	1	3	0	1	1	3	0
L4	0	0	2	0	0	3	1	2
Vertical Bound	0	0	0	0	0	1	2	0
Total	3	3	21	17	16	22	9	7

Substrate orientations used for different locomotor modes by indri group 40

Orientation of substrate influences indri movement (χ^2=53.2, df=2, p<0.001). Lenore used vertical substrates for movement more than fifty percent of the time (Table 6.97), primarily by moving with one and two meter leaps. Interestingly, Lenore used all orientations for her longer distance leaps. She made four meter leaps onto adjacent trees using horizontal substrates as interim springboards to reach her next area of movement.

Table 6.97 Substrate orientation and locomotor modes used by indri group 40

Orientation	Horizontal	Oblique	Vertical
Climb	0	1	5
L1	4	9	26
L2	4	5	23
L3	0	4	5
L4	2	2	4
Vertical Bound	0	1	3
Total	10	22	66

Quadrant use for movement by indri group 40

Indri moving behavior is influenced by tree quadrant (χ^2=188.4, df=5, p<0.001). Lenore mainly occupied quadrant 7 for movement (Table 6.98) using one (66.7%) and two (65.6%) meter leaps.

Table 6.98 Movement in varying quadrants by indri group 40

Quadrant	1	2	3	4	5	6	7	Liana
Move (N)	2	0	0	3	5	20	65	3

Canopy/vegetation connectivity and locomotor modes by indri group 40

The level of canopy/vegetation connection affects moving behavior (K-S, D_{MAX}=0.18, p<0.01). Lenore mainly moved through areas with connected canopy/vegetation (51.0%) and to a lesser extent small-gapped (33.7%) and medium gapped areas (15.3%) (Table 6.99). The degree of connectivity affects Lenore's mode of locomotion (χ^2=6.2, df=2, p<0.05). In areas of connected forest Lenore used one meter leaps more frequently (Table 6.100). In non-connected forest Lenore used more of her three and four meter leaps. Lenore mainly moved by between-substrate movement (88.5%) (Figure 6.8) again via one and two meter leaps. Within-substrate movement consisted more so of climbing and vertical bounding forms of movement.

Table 6.99 Different levels of canopy connectedness and movement by indri group 40

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Move (N)	50	0	33	0	15

Table 6.100 Levels of canopy connectedness and locomotor modes by indri group 40

Distance b/n Canopy	Connected	Small	Medium	Total
Climb	1	1	4	6
L1	27	10	2	39
L2	16	13	3	32
L3	4	3	2	9
L4	2	3	3	8
Vertical Bound	0	3	1	4
Total	50	33	15	98

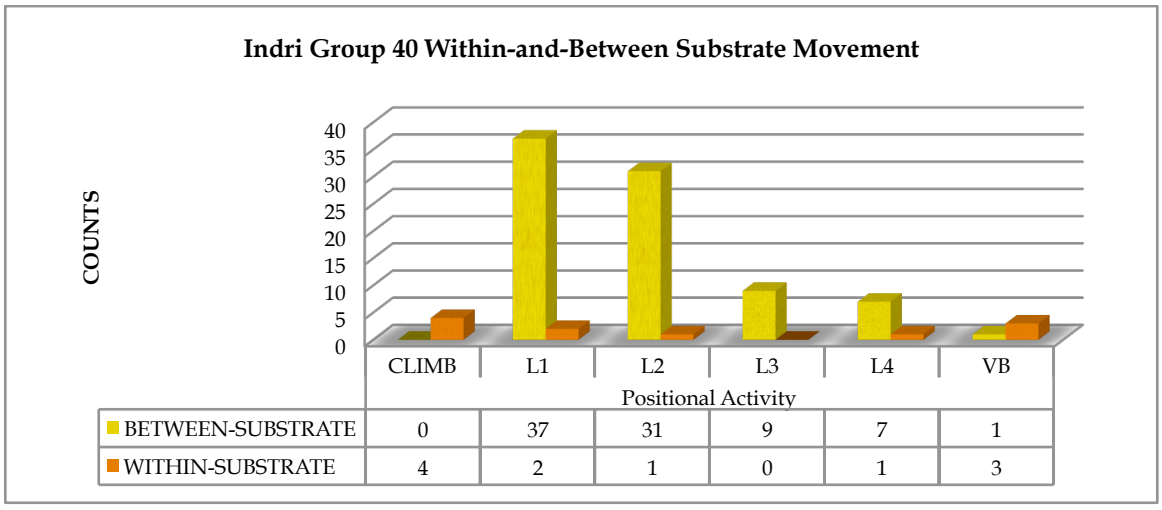


Figure 6.8 Indri Group 40 Within-and-between substrate movement

RESTING BEHAVIOR BY INDRI IN GROUP 40

Postures used for resting by indri group 40

Lenore rested primarily in a sit-extend posture (45.0%) (Table 6.101).

Table 6.101 Postural modes used while resting for indri group 40

Postural Modes for Rest (N=817)	Total Count	Percentage
Recline	32	3.9%
Sit-Extend	368	45.0%
Sit	231	28.3%
Vertical Cling	186	22.8%

Size of substrate used for resting by indri group 40

Indri resting behaviors are influenced by the size of substrate (K-S, D_{MAX}=0.24, $p<0.01$). Lenore frequently rested on medium (42.8%) and large (30.7%) sized substrates (Table 6.102).

Table 6.102 Different sized substrates used for resting behaviors by indri group 40

Size of Substrate Resting	Total Count	Percentage
Very Small (<1 cm)	20	2.5%
Small (1-5 cm)	188	23.9%
Medium (6-10 cm)	337	42.8%
Large (11-15 cm)	242	30.7%
Total	787	100%

Size of substrate used for different resting postural modes by indri group 40

Lenore mainly assumed a sit-extend position on medium (45.9%) or large (28.0%) substrates, a sit on small (29.0%), medium (33.3%), and large (36.4%) substrates, and most of her vertical clinging occurred on medium (48.9%) substrates (Table 6.103).

Table 6.103 Substrate sizes used for different postures by indri group 40

Size of Substrate	Very Small	%	Small	%	Medium	%	Large	%	Total
Recline	1	50%	1	50%	0	0%	0	0%	2
Sit-Extend	15	4.1%	81	22.0%	169	45.9%	103	28.0%	368
Sit	3	1.3%	67	29.0%	77	33.3%	84	36.4%	231
VC	1	0.5%	39	21.0%	91	48.9%	55	29.6%	186
Total	20		188		337		242		

Substrate orientation used for resting by indri group 40

Indri resting behaviors are influenced by orientation of substrate (χ^2=220, df=2, p<0.001). Lenore used oblique substrates more than half of the time for resting behavior (Table 6.104). Almost all resting on horizontal branches was a sit or sit-extend (98.5%) postures as well as with oblique substrates (76.5%). Resting while vertical clinging also occurred on oblique substrates (23.3%), but this behavior mostly occurred on vertical substrates (92.2%).

Table 6.104 Different orientations used for resting behaviors by indri group 40

Horizontal Count	%	Oblique Count	%	Vertical Count	%	Total
267	33.9%	430	54.6%	90	11.4%	787

Height of substrate and resting behavior by indri group 40

Indri resting behaviors are influenced by substrate height (K-S, D_{MAX}=0.08, p<0.01). Lenore frequently rested at a height of 10 meters, although she also spent time resting at the heights of 4 to 5 meters as well as 12 to 13 meters (Table 6.105).

Table 6.105 Height of substrate used while resting for indri group 40

Height of Substrate	A	B	C	D	E	F	G	H	I
Rest	2	40	132	93	67	187	90	150	26

Quadrant use and resting behavior by indri group 40

Indri have a preference for certain quadrants for resting (χ^2=1350, df=7, p<0.001). Lenore rested in all quadrants, even on lianas, but spent more than half her time resting in quadrant 6 (54.1%) (Table 6.106).

Table 6.106 Different quadrants used for resting by indri group 40

Quadrant	1	2	3	4	5	6	7	Liana	Knot
Rest	3	36	35	57	105	426	109	16	0

Canopy/vegetation connectivity and resting behaviors by indri group 40

Canopy/vegetation connectedness affects indri resting behavior (K-S, D_{MAX}=0.2, p<0.01). Lenore rested more frequently in areas with connected canopy/vegetation (40.0%) and less frequently in areas with connected/small gaps (1.3%) (Table 6.107).

Table 6.107 Distances in canopy used for resting behaviors by indri group 40

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	315	10	201	65	196

INDRI GROUP 40 SUBSTRATE COMBINATIONS AND NEAREST NEIGHBOR

Substrate Combinations

Orientation of substrate and quadrant use by indri group 40

Lenore used horizontal substrates more frequently in quadrants 1 and 5 whereas oblique substrates were used more so in quadrants 4, 6, and 7 (Table 6.108). Vertical substrates were used the most in quadrant 7.

Table 6.108 Orientation and quadrant used by indri group 40

Quadrant	Horizontal	Oblique	Vertical
1	17	3	0
2	41	44	0
3	41	45	0
4	94	153	10
5	213	10	2
6	183	364	22
7	5	57	197
Liana	6	14	4
Knot	0	0	11

Height of substrate and quadrant use by indri group 40

Lenore utilized quadrants 4 and 6 at the height of 9 to 10 meters (Table 6.109). At the height of 11 meters quadrants 4, 5, and 6 were used relatively equally. Lenore also frequently used quadrant 5 at the taller heights of 12 to 15 meters.

Table 6.109 Quadrant and height used by indri group 40

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Liana	Knot
A							8		
B				8	1	46	26	4	8
C			2	17		89	88	13	
D		5		18	26	98	46		
E	1	13	36	19	5	68	40	4	3
F		2	5	118	9	182	32	2	
G	4	4	6	36	54	44	13		
H	14	52	37	34	104	42	6	1	
I	1	9		7	26				

Total tree height and height of substrate used by indri group 40

Lenore used a full range of different height of substrate and total height of tree combinations (Table 6.110). Shorter trees often have less crown volume and taller trees often, but not always, have more crown volume. As such, when Lenore occupied shorter trees she often used the lower quadrants due to limited choice of space but when she used taller heights with greater crown volume she monopolized the higher components of the canopy.

Table 6.110 Height of substrate and total height of tree used by indri group 40

Height of tree	B	C	D	E	F	Fallen Tree	G	H	I
Height of Substrate									
A		2	2	4					
B	3	8	1	39	21		21		
C		5	56	34	56	7	51		
D			21	62	91		17	2	
E				19	139		31		
F			2		69		206	73	
G							23	121	17
H					6			254	30
I								1	42

Keystone Structures

The home range that Lenore used was eclectic and consisted of areas of dense 1-5 cm dbh trees, valleys of apanga and pandanus palms, areas of trees falls and abundant lianas, and areas of 15 meter plus canopy. Lenore used important keystone structures in her environment that are presented in Table 6.111. Lenore often recycled the same trees for feeding, resting, and moving. For example, one day she may feed from the tree and the next use it as a moving structure with no feeding behaviors. Lenore also had an affinity for tree knots and used them quite frequently as feeding substrates.

Table 6.111 Keystone structures used by indri group 40

Malagasy Tree	Dbh (cm)	Height (m)	Activity	GPS
Azinina	12	9.8	Feeding leaves	(0309676, 8018325)
Azinina	8	7.1	Feeding leaves Resting/Moving	(0309803, 8018456)
Trova	24	11.3	Feeding leaves	(0309884, 8018389)
Hazoaraka	43	11.9	Moving/Resting	(0309884, 8018389)
Voapaka beravina	29	12.2	Feeding leaves Moving/Resting	(0309860, 8018352)
Tavolo mena	45	11.7	Feeding leaves	(0309780, 8018301)

Indri Group 40 Summary Statement:

Certain microhabitat features influenced Lenore's movement, feeding, and resting behaviors. However, Lenore's movement was not affected by the size of substrate or the height of substrate. These paragraphs highlight those substrates that Lenore utilized at a higher frequency than others, but as noted in the preceding sections, Lenore was capable of utilizing a wide range of different heights and substrates for resting, eating, and moving. Overall Lenore spent almost equal percentages of her time eating and resting with the least amount of time dedicated to moving or other correlated behaviors. Summarizing all behaviors, Lenore commonly occupied medium-sized horizontal and oblique substrates at a height of 10 meters in quadrant 6. The total tree height she used was 9 to 13 meters. During each all day follow the substrates that Lenore used were flagged and identified when possible. The list of the trees that Lenore frequently used for resting, moving, and feeding is included in the appendix. Lenore used a variety of tree species, but showed a heightened preference for some trees more so than the other lemur groups. She incorporated the same keystone structures for resting, moving, and feeding on a regular basis. For feeding Lenore focused on rara (N=15), tavolo fotsy (N=8), and azinina (N=8) leaves. Overall, the most common trees Lenore used for all behaviors included rara (N=24), azinina (N=16), tavolo fotsy (N=13), lalotina (N=10), and mampay (N=10).

Out of the total amount of time Lenore spent feeding, she dedicated the highest percentages of time to eating mature leaves and young leaves while sitting on medium horizontal or oblique substrates in quadrant 4 at a wide range of heights (6 to 13 meters). Lenore primarily engaged in feeding behaviors in areas with connected canopy/vegetation.

Lenore moved through the connected forest using one and two meter leaps on small, medium, and large vertical substrates equal proportions of the time. Although Lenore did focus her two meter leaps more so on medium and large substrates. Lenore moved between the height range of 4 and 10 meters throughout the forest. Lenore's pathway often seemed an indirect route to the

feeding or resting tree and she rarely took the same path twice. All day follows with Lenore often involved exploring new areas that had not been traveled through during the previous follow.

Lenore rested in sit-extend postures on medium and large oblique substrates at a height of 10 meters in quadrant 6 in areas of connected canopy/vegetation. Lenore groomed herself for extended periods before and after rest, more so than other indri in other groups.

Lenore used horizontal substrates within the peripheral quadrants of the tree and oblique substrates in quadrants closer to the trunk of the tree. Lenore used a variety of different quadrant and tree height combinations with the most frequent use occurring in quadrants 4 and 6 at a height of 9 to 10 meters and quadrant 5 at the taller heights in the canopy. Moreover, Lenore also used a full range of different height of substrate and total height of tree combinations. When taller trees were occupied Lenore also used taller substrates, maximizing her use of the entire tree crown.

Lenore was flexible in her ability to utilize a wide spectrum of different substrates, orientations, and heights for resting, feeding, and moving behaviors. Lenore demonstrated one of the few instances where the height and size of substrate did not have an affect on moving patterns. Lenore appeared to have a heightened preference for certain substrates, especially for resting behaviors, but she was also able to make adjustments and use other forest elements.

Subsection 6.5
INDRI GROUP 50

INDRI GROUP 50: Group composition consisted of one adult male (George), three adult females (named after collar color) and one juvenile male (Steve).
Male radio collar. 6.5 kg, body length 44.0 cm, tail 6.0 cm.
Female green collar. 6.6 kg, body length 50.0 cm, tail length 6.5 cm.
Juvenile male no collar. 3.3 kg, body length 41.5 cm, tail 4.5 cm.
Female no collar. 7.1 kg, body length 53.0 cm, tail 7.0 cm.
Female light blue/teal collar. 5.4 kg, body length 52.0 cm, tail 5.8 cm

Overall size of substrate: A 0.1%, B 19.7%, C 71.8%, D 8.4%
Overall height of substrate: A 2.3%, B 5.4%, C 3.4%, D 10.4%, E 18.9%, F 22.8%, G 19.4%, H 4.6%, I 12.8%
Overall quadrant: Quad1 9.0%, Quad2 3.2%, Quad3 19.7%, Quad4 7.4%, Quad5 14.9%, Quad6 35.0%, Quad7 9.6, Fallen Branch 0.1%, Knot 0.1%, Liana 0.8%, Tree cluster 0.3%
Overall orientation: A 47.5%, B 44.2%, C 8.4%
Total activity budget: Eat fruit 0.3%, Eat flowers 3.4%, Eat leaves 21.1%, Eat young leaves 3.8%, Groom other 0.4%, Groom-self 3.2%, Kiss 0.1%, Move 5.0%, Rest 62.7%.
Total tree height: B 1.2%, C 3.4%, D 2.2%, E 6.6%, F 30.5%, G 27.5%, H 15.3%, I 0.4%, J 12.9%

Indri group 50 was the largest group of indri followed or observed in this research. The radio-collar was placed on the male and so many of the behavioral observations are based on his activity budget. Indri group 50 spent more time resting in comparison to feeding or moving behaviors (Figure 6.9). This was also the highest percentage of time dedicated to resting in comparison to the other lemur groups.

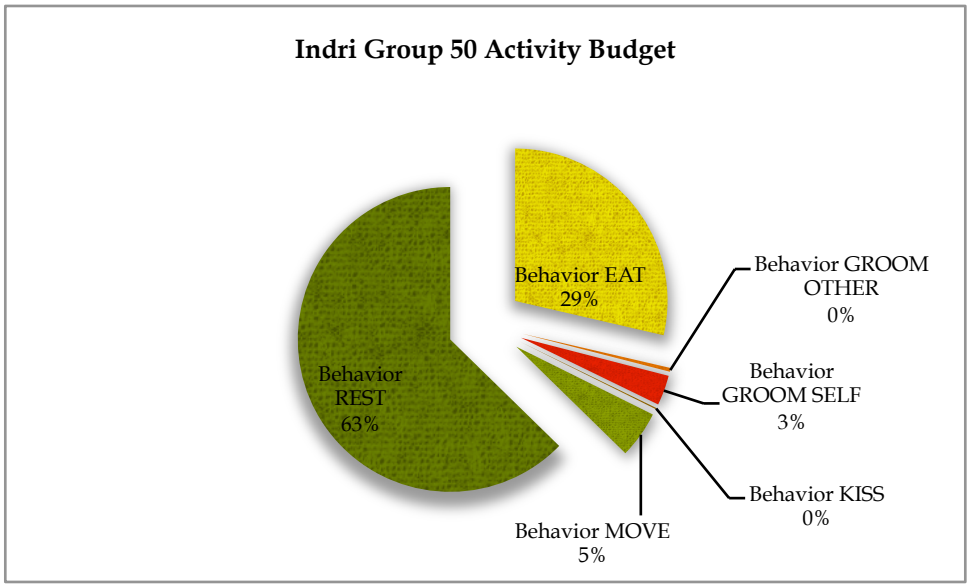


Figure 6.9 Indri group 50 activity budget.

FEEDING BEHAVIORS BY INDRI GROUP 50

Types of foods consumed by indri group 50

Indri group 50 consumed mature leaves frequently in their diet (73.8%) (Table 6.112). The percentage of flowers (11.8%) and young leaves (13.2%) in the diet was relatively equal.

Table 6.112 Foods consumed by indri group 50

Food (N=431)	Total Count	Percentage
Fruit	5	1.2%
Flowers	51	11.8%
Mature Leaves	318	73.8%
Young Leaves	57	13.2%

Postures used for the consumption of different foods by indri group 50

Feeding by indri was in a sit posture over 50% of the time (Table 6.113) where all of the food types eaten by indri group 50 were consumed. Suspensory and recline postures were used to eat young and mature leaves while sit extend and vertical-cling postures were used more flower consumption (Table 6.113).

Table 6.113 Postures used for food consumption by indri group 50

Posture (N=434)	Total Count	Percentage	Food eaten in posture	Percentage
Recline	10	2.3%	EL, EYL	70%, 30%
Sit Extend	106	24.4%	EFL, EL, EYL	38.5%, 46.2%, 15.4%
Sit	279	64.3%	EF, EFL, EL, EYL	1.4%, 12.9%, 78.9%, 6.8%
Suspend	7	1.6%	EL, EYL	57.1%, 42.9%
Vertical Cling	32	7.4%	EF, EL, EYL	3.1%, 15.6%, 81.3%

Size of substrate used by indri group 50 while feeding

Indri group 50 used medium substrates for feeding behaviors more than 50% of the time (64.3%). Indri 50 rarely used very small or large substrates (Table 6.114).

Table 6.114 Different sized substrates used for food consumption by indri group 50

Size of Substrate Used in Feeding	Count	Percentage of Use
Very Small (<1cm)	1	0.2%
Small (1-5 cm)	124	28.8%
Medium (6-10cm)	277	64.3%
Large (11-15 cm)	29	6.7%

Height of substrate used by indri group 50 while feeding

Indri group 50 fed within a wide height range, but a higher frequency occurred between the heights of 9 to 11 meters (Table 6.115). Most of the flower consumption occurred at a height of 11 meters (84.3%). Leaves were eaten at all heights, but with a focus on mature leaves at a height of 9 to 10 meters (26.3%) as well as 11 meters (29.2%). Young leaves were eaten at the heights of one meter (26.3%) and 9 to 10 meters (45.6%) (Table 6.115).

Table 6.115 Height of substrate used for food consumption by indri group 50

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	19	4.4%
B (2-3 m)	6	1.4%
C (4-5 m)	16	3.7%
D (6 m)	26	6.0%
E (7-8 m)	14	3.2%
F (9-10 m)	133	30.9%
G 11 (m)	136	31.6%
H (12-13 m)	48	11.1%
I (14-15 m)	33	7.7%
Total	431	100%

Orientation of substrate used by indri group 50 while feeding

Indri used oblique substrates more frequently for feeding behaviors (51.0%) (Table 6.116). This higher oblique percentage is the result of a focus on mature leaves while occupying this orientation. Flower consumption primarily was on horizontal substrates (70.6%), while young leaf consumption occurred at a higher percentage on horizontal (36.8%) and vertical substrates (47.4%).

Table 6.116 Orientation of substrate used for food consumption by indri group 50

Food	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%	total
Fruit	0	0%	4	80%	1	20%	5
Mature Leaves	122	38.4%	192	60.4%	4	1.3%	318
Flowers	36	70.6%	15	29.4%	0	0%	51
Young Leaves	21	36.8%	9	15.8%	27	47.4%	57

Use of different tree quadrants while feeding by indri group 50

Flowers were mainly consumed in quadrants one and two (66.7%). Leaves were consumed in all quadrants with a focus on quadrants 1 and 3 (50.6%). Young leaves were consumed more frequently in quadrants 5 and 7 (84.2%) (Table 6.117).

Table 6.117 Quadrant used for food consumption by indri group 50

Quadrant	1	2	3	4	5	6	7	Liana	Liana/Tree Tangle	Total
Fruit	0	0	0	0	0	4	1	0	0	5
Flowers	21	13	0	9	0	8	0	0	0	51
Mature Leaves	85	18	76	51	35	41	4	4	4	318
Young Leaves	0	0	0	8	23	0	25	1	0	57
Total	106	31	76	68	58	53	30	5	4	431

Foods consumed in different levels of canopy/vegetation connectivity by indri group 50

Indri group 50 frequently engaged in feeding behaviors in forested areas with connected canopy/vegetation (32.6%), as well as in areas with medium/large gaps (25.5%). Thirty-three percent of indri group 50's leaf consumption occurred in areas with medium/large gaps (Table 6.118).

Table 6.118 Canopy/vegetation distances and foods consumed by indri group 50

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium	TOTAL
Eat Fruit	5	0	0	0	0	5
Eat Flowers	38	0	13	0	0	51
Eat Mature Leaves	39	82	77	0	100	298
Eat Young Leaves	52	0	0	0	5	57
TOTAL	134	82	90	0	105	411

LOCOMOTION BY INDRI GROUP 50

Locomotor modes used by indri group 50

Overall, indri in group 50 spent 63% of their time resting and only 5% of their time moving. Indri group 50 mainly moved by leaping distances of varying lengths. Most of the leaps were one (46.6%) or two (32.9%) meters in length (Table 6.119).

Table 6.119 Locomotor modes used by indri group 50

Locomotor Modes (N=73)	Total Count	Percentage
Climb	1	1.4%
L1	34	46.6%
L2	24	32.9%
L3	11	15.1%
L4	2	2.7%
Vertical Bound	1	1.4%
TOTAL	73	100%

Size of substrate used for locomotion by indri group 50

Size of substrate affects indri movement (K-S, D_{MAX}=0.23, $p<0.01$). Indri in group 50 were capable of using a range of different sized substrates for moving behaviors, but the overwhelming focus was on medium substrates (68.0%) (Table 6.120) by one and two meter leaps (Table 6.121).

Table 6.120 Different sized substrates for movement by indri group 50

Size of Substrate	Very small	Small	Medium	Large
Move	1	15	51	8

Table 6.121 Different locomotor modes on varying sized substrates by indri group 50

Size of Substrate	Very Small	Small	Medium	Large	Total
Climb	0	0	1	0	1
L1	1	9	23	1	34
L2	0	4	17	5	26
L3	0	1	8	2	11
L4	0	1	1	0	2
Vertical Bound	0	0	1	0	1
Total	1	15	51	8	75

Heights used by indri group 50 for locomotion

Height of substrate affects indri movement (K-S, D_{MAX}=0.18, $p<0.05$). Indri 50 moved at a range of heights but focused most of their movement between the heights of 6 and 10 meters (Table 6.122). Indri used a variety of leaping distances across all heights (Table 6.123).

Table 6.122 Different heights used for movement by indri group 50

Height of Substrate	A	B	C	D	E	F	G	H	I
Move	3	8	4	10	20	20	8	0	2

Table 6.123 Different heights and locomotor modes used by indri group 50

Height of substrate	A	B	C	D	E	F	G	H	I	TOTAL
Climb	0	0	0	1	0	0	0	0	0	1
L1	3	7	0	6	7	7	4	0	0	34
L2	0	0	3	2	8	10	1	0	2	26
L3	0	1	1	1	4	1	3	0	0	11
L4	0	0	0	0	0	1	0	0	0	1
Vertical Bound	0	0	0	0	0	1	0	0	0	1
Total	3	8	4	10	20	20	8	0	2	75

Substrate orientations used for different locomotor modes by indri group 50

Orientation of substrate influences indri movement (χ^2=30, df=2, p<0.001). Indri in group 50 used vertical substrates for movement more than 60% of the time, using all leaping distances. Horizontal or oblique substrates were used for shorter distance leaps (Table 6.124).

Table 6.124 Locomotor modes used on varying oriented substrates by indri group 50

Orientation	Horizontal	Oblique	Vertical
Climb	0	0	1
L1	5	10	19
L2	1	12	13
L3	0	0	11
L4	0	1	1
Vertical Bound	0	1	0
Total	6	24	45

Quadrant use for movement by indri group 50

Indri movement is influenced by tree quadrant (χ^2=112, df=5, p<0.001). Indri in group 50 occupied quadrant 7 60% of the time for movement using one and two meter leaps (65.0%) (Table 6.125).

Table 6.125 Movement in varying quadrants by indri group 50

Quadrant	1	2	3	4	5	6	7	Fallen Branch
Move	3		1	5	4	16	45	1

Canopy/vegetation connectivity and locomotor modes by indri group 50

The level of canopy/vegetation connectedness affects indri movement (K-S, D_{MAX}=0.21, p<0.01). Indri in group 50 frequently moved through connected canopy/vegetation (45.0%) areas of the forest and rarely moved through areas with medium gaps (5.3%) (Table 6.126). However, canopy/vegetation connectedness does not affect the locomotor mode used to negotiate the gaps in the forest (χ^2=0.86, df=2, p>0.05). When the indri moved through medium-gapped areas, the indri

still moved by one and two meter leaps (Table 6.127). Most of the movement by indri group 50 was between-substrate movement via one and two meter leaps (Figure 6.10).

Table 6.126 Different levels of canopy connectedness and movement by indri group 50

Distance b/n Canopy	A	B	C	D	E
MOVE (N)	34	19	18	0	4

Table 6.127 Levels of canopy connectedness and locomotor modes used by indri group 50

Distance b/n Canopy	A	B	C	E	Total
Climb	0	0	1	0	1
L1	17	9	7	1	34
L2	10	7	6	3	26
L3	6	2	3	0	11
L4	1	1	0	0	2
Vertical Bound	0	0	1	0	1
Total	34	19	18	4	75

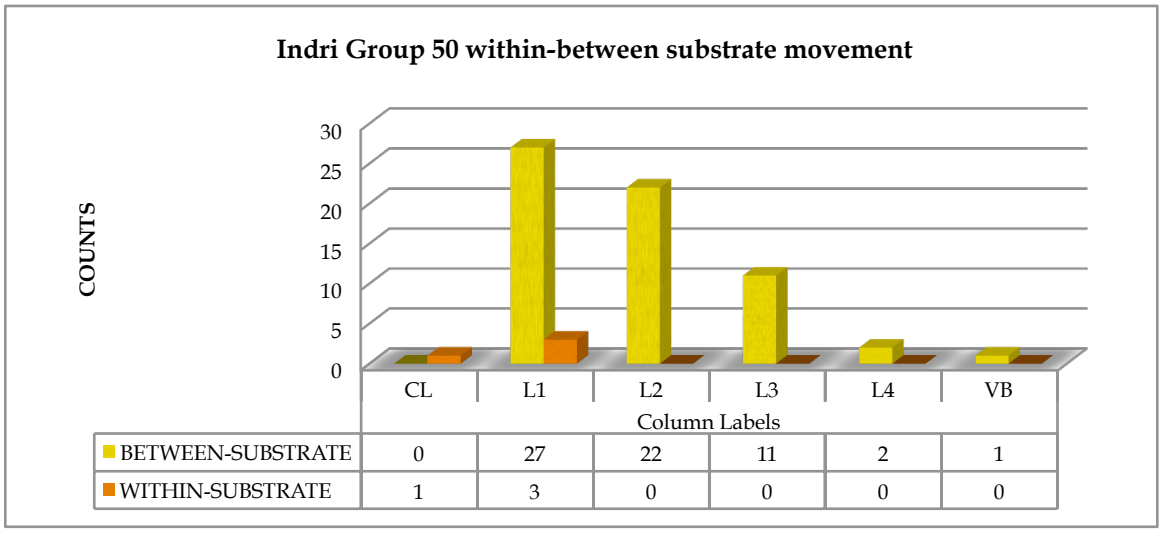


Figure 6.10 Indri group 50 within-and-between substrate movement

RESTING BEHAVIORS BY INDRI GROUP 50

Postures used for resting by indri group 50

Indri group 50 commonly assumed a sit posture (57.2%) followed by a sit-extend (27.4%) for resting behaviors (Table 6.128).

Table 6.128 Postural modes used while resting by indri group 50

Postural Modes for Rest (N= 944)	Total Count	Percentage
Recline	55	5.8%
Sit Extend	259	27.4%
Sit	540	57.2%
Vertical Cling	90	9.5%

Size of substrate used for resting by indri group 50

Indri resting behaviors are influenced by size of substrate (K-S, D_{MAX}=0.28, p<0.01). Indri group 50 focused on medium substrates (76.2%) for resting behaviors (Table 6.129).

Table 6.129 Different sized substrates used for resting by indri group 50

Size of Substrate Resting	Total Count	Percentage
Small (1-5 cm)	146	15.5%
Medium (6-10 cm)	719	76.2%
Large (11-15 cm)	79	8.4%
Total	944	100%

Size of substrate used for different resting postural modes by indri group 50

Reclining postures for rest often occurred on medium and large substrates. Indri group 50 focused the remainder of their resting postures on medium substrates although they showed the flexibility of using all three sizes in some capacity (Table 6.130)

Table 6.130 Different sized substrates for resting postures by indri group 50

Size of Substrate	Small	%	Medium	%	Large	%	Total
Recline	0	0%	27	49%	28	50.9%	55
Sit-Extend	52	20.1%	195	75.3%	12	4.6%	259
Sit	80	14.8%	435	80.6%	25	4.6%	540
VC	14	15.6%	62	68.9%	14	15.6%	90

Substrate orientation used for resting by indri group 50

The orientation of substrate influences resting behaviors (χ^2=358, df=2, p<0.001). Half of the resting behaviors by indri 50 occurred on horizontal substrates. The other half was dominated

by the use of oblique (41.5%) and to a lesser extent, vertical (5.1%) substrates (Table 6.131). The main posture for rest on horizontal substrates was a sit (71.0%).

Table 6.131 Different orientations used for resting behaviors by indri group 50

Horizontal Count	%	Oblique Count	%	Vertical Count	%	Total
504	53.4%	392	41.5%	48	5.1%	944

Height of substrate and resting behaviors by indri group 50

Indri resting behaviors are influenced by substrate height (K-S, D_{MAX}=0.22, p<0.01). Indri group 50 rested at a range of heights with more time spent resting at a height of 7 and 8 meters (24.5%) and 9 and 10 meters (19.6%) (Table 6.132).

Table 6.132 Different heights of substrates for resting by indri group 50

Height of Substrate	A	B	C	D	E	F	G	H	I
Rest	12	63	28	119	226	181	138	22	155

Quadrant use and resting behavior by indri group 50

Indri have a preference for certain quadrants for resting behaviors (χ^2=1832, df=7, p<0.001). The most common quadrant for rest was quadrant 6 (44.7%) while the least visited quadrant for rest was quadrant 2 (1.6%) (Table 6.133).

Table 6.133 Different quadrants used for resting by indri group 50

Quadrant	1	2	3	4	5	6	7	Knot	Liana
Rest	27	15	211	38	152	422	70	2	7

Canopy/vegetation connectivity and resting behaviors by indri group 50

Canopy/vegetation connectivity affects indri resting behavior (K-S, D_{MAX}=0.23, p<0.01). The indri in group 50 frequently rested in areas of connected canopy/vegetation (42.9%), although they were capable of resting within all of the connectedness categories (Table 6.134).

Table 6.134 Distances in canopy used for resting behaviors by indri group 50

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	405	129	159	71	180

INDRI GROUP 50 SUBSTRATE COMBINATIONS AND KEYSTONE STRUCTURES

Substrate Combinations

Orientation of substrate and quadrant use by indri group 50

Indri group 50 used oblique substrates more frequently in quadrants 1, 6, 7, and on lianas (Table 6.135). The use of horizontal substrates was more prominent in quadrants 3 and 5. The use of vertical substrates mainly occurred in quadrant 7 (Table 6.135).

Table 6.135 Orientation and quadrant used by indri group 50

Quadrant	Horizontal	Oblique	Vertical
1	39	97	0
2	27	21	0
3	262	34	0
4	25	79	7
5	175	47	2
6	178	338	11
7	5	36	104
Fallen Branch	0	1	0
Knot	0	0	2
Liana	0	12	0
Tree Cluster	4	0	0

Height of substrate and quadrant use by indri group 50

When indri individuals were lower in the canopy at a height of one meter they were only observed and recorded to use quadrant 7. At a height of 7 meters and taller the indri used more of

the quadrants in the tree canopy (Table 6.136). At a height of 11 meters the indri frequently used quadrant 1 (34.2%) and quadrant 3 at a height of 14 to 15 meters (89.6%) (Table 6.136).

Table 6.136 Height of substrate and quadrant use by indri group 50

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Fallen Branch	Knot	Liana	Tree Cluster
A	0	0	0	0	0	0	34	0	0	0	0
B	0	0	0	2	0	62	12	0	2	3	0
C	0	0	0	1	7	24	15	0	0	0	4
D	0	0	9	2	28	97	21	0	0	0	0
E	0	0	0	7	129	115	30	1	0	2	0
F	11	1	30	41	60	187	9	0	0	5	0
G	100	27	78	37	0	30	20	0	0	0	0
H	25	4	6	21	0	10	2	0	0	2	0
I	0	16	173	0	0	2	2	0	0	0	0

Total tree height and height of substrate used by indri group 50

Indri group 50 used a full range of different height of substrate and total height of tree combinations. Shorter trees often have less crown volume and taller trees often, but not always, have more crown volume. As such, when the indri occupied shorter trees they often used the lower quadrants perhaps due to limited choice of space. When the indri used taller heights with greater crown volume they monopolized the higher components of the canopy. Especially at a height of 11 meters indri 50 used a broad range of substrate heights, maximizing their use of the available space in the tree crown. Though at the tallest heights, the indri also used the tallest available substrates (Table 6.137).

Table 6.137 Height of substrate and total height of tree used by indri group 50

Height of tree	B	C	D	E	F	G	H	I	J
Height of Substrate									
A	12	4	9	9					
B	6	47	3	14	8	4			
C			14	12	22	3			
D			7	54	4	1			
E				10	202	66	6		
F				1	133	189	21		
G						151	141		
H							62	6	2
I									193

Keystone Structures

One of the areas frequented by the indri included a near dead pallisandre tree growing in an area that also included multiple dead trees and abundant detritus on the forest floor. The indri fed on the young leaf growth of new growth trees (<2 meters) while vertical-clinging to adjacent dead trees with larger dbh's. Some of the keystone substrates the indri in group 50 used were also used several times by the sifaka in group 10 (e.g. rara tree, azinina tree). As noted previously, this indri group spent a large percentage of their time resting. Therefore, many of their keystone structures were resting trees that were used on a regular basis. The keystone structures used by indri group 50 are presented in Table 6.138.

Table 6.138 Keystone structures used by indri group 50

Malagasy Tree	Dbh (cm)	Height (m)	Activity	GPS
Rara	52	6.9	Feeding leaves Resting	(0309459, 8018247)
Rara	8	7.8	Moving/Resting	(0309361, 8018336)
Azinina	8	5.6	Moving/Resting	(0309328, 8018334)
Antafonona	22	10.4	Feeding leaves	(0309272, 8018299)
Rara	32	10.6	Moving/Resting	(0309272, 8018299)
Hazoboangy	22	10.9	Feeding leaves	(0309184, 8018249)
Antafonona	5	1.9	Feeding young leaves	(0309184, 8018249)
Rara	10	8.7	Feeding leaves	(0309199, 8018142)

INDRI 50 NEAREST NEIGHBOR

Identity of nearest neighbor

The juvenile was the nearest neighbor to the radio-collared focal male more than half of the time (Table 6.139). The female with the blue collar was the nearest neighbor the most frequent out of all of the other adults (18.7%). The male did go off on his own some full days or for portions of days where he was more than 20 meters away from the other group members (23.7%).

Table 6.139 Nearest neighbor indri group 50

Nearest Neighbor	Focal Male
All	18
Blue	261
Blue/Green	2
Green	13
Green/Juvenile	9
Juvenile	762
>20 m	331

Distance of nearest neighbor

The juvenile's distance from the focal male ranged from contact up to 10 meters with the most common distance being six meters. The female with the blue collar also had a wide range of distances from contact up to 15 meters. No pattern emerged, making a table uninformative.

Indri Group 50 Summary Statement

Microhabitat features influence indri group 50 movement, feeding, and resting behaviors. These paragraphs highlight those substrates that indri group 50 utilized at a higher frequency than others, but as noted in the preceding sections, the indri in this group were capable of utilizing a wide range of different heights and substrates for resting, eating, and moving. In summary, indri group 50 used medium substrates at the heights of 7 to 11 meters in quadrant 6 on horizontal branches. A majority of their time was spent resting and feeding with little time devoted to moving.

The total tree height mainly used by indri group 50 ranged from 10 to 12 meters. During each of the all day follows the substrates that this group used were flagged and identified when possible. The list of the trees used for resting, moving, and feeding is included in the appendix. Indri group 50 used a variety of tree species but showed a heightened preference for some trees more so than others. Indri in group 50 included important keystone structures for resting, feeding, and moving behaviors on a routine basis. Some of the keystone substrates the indri in group 50 used were also used several times by the sifaka in group 10. For feeding behaviors group 50 focused on rara leaves and fruits (N=19) and anatafonona flowers and leaves (N=9). Overall, the most common trees group 50 used for all behaviors included rara (N=23), azinina (N=8), longotra (N=6), tavolo fotsy (N=10), and antafonona (N=9).

Indri in group 50 consumed mature leaves the most frequently in their diet and lesser, equal amounts of time were dedicated to flowers and young leaves. Feeding postures by indri group 50 were dominated by a sit on medium oblique branches at a height of 9 to 11 meters in quadrants 1 and 3. The indri often fed in areas with connected canopy/vegetation as well as medium-gapped forested areas.

Indri in group 50 spent 5% out of their total activity budget moving. Indri mainly moved by leaping one and two meter distances onto medium vertical substrates at a height range between 6 and 10 meters in quadrant 7. Indri frequently moved through connected canopy vegetation areas of the forest and rarely through areas with medium gaps.

Indri in group 50 assumed a sit position quite often for resting behaviors on medium horizontal substrates at a height ranging from 7 to 10 meters. The indri commonly rested in quadrant 6 in connected canopy/vegetation areas.

Indri used horizontal substrates more frequently in quadrants 3 and 5, whereas the use of oblique substrates was more prominent in quadrants 1, 6, and 7. When the indri were lower in the canopy at a height of one meter they commonly occupied quadrant 7. But at a height of 7 meters

and taller, the indri used more of the quadrants in the tree canopy. Especially at a height of 11 meters, indri group 50 used a broad range of substrate heights maximizing their use of the available space in the tree crown. However, when the indri used some of the tallest trees heights (+16 meters) the indri often exploited the tallest available substrates.

Indri group 50 were more traditional in their quadrant choices and use of substrates, meaning that they mainly used the tree canopy and trunk and only occasionally made use of lianas, for resting, feeding, and moving behaviors. Indri group 50 rarely incorporated the use of other substrates in their environment.

When the male was the focal animal the juvenile was often the nearest neighbor followed by the female with the blue collar. The one social interaction that I observed in this group was between the radio-collared male and female with the blue collar. The social interaction involved sitting in close contact and mutually grooming one another for several minutes. The male also spent entire or partial days alone, only to reconvene with his group later in the day.

Indri group 50 were more restricted in the substrates used for resting, moving, and feeding behaviors. This is especially true in their limited use of quadrants, making use primarily of the tree crown and trunk and rarely expanding out to incorporate other substrates into their behavioral repertoire.

Subsection 6.6
INDRI GROUP 14

INDRI GROUP 14: Group composition consisted of one adult female (Fran), one adult male (Ernie), and one female juvenile (Violet).
Female radio collar. 8.4 kg, body length 57.0 cm, tail length 4.0 cm.
Male faded red collar with gold medallion. 7.3 kg, body length 51.0 cm, tail 3.9 cm.
Female juvenile not collared. 3.8 kg, body length 46.5 cm, tail 3.0 cm

Overall size of substrate: A 0.4%, B 19.1%, C 73.2%, D 6.9%
Overall height of substrate: A 0.6%, B 1.0%, C 3.5%, D 6.3%, E 18.1%, F 32.8%, G 13.9%, H 23.4%
Overall quadrant: Quad1 6.6%, Quad2 5.9%, Quad3 6.2%, Quad4 23.1%, Quad5 19.4%, Quad6 24.4%, Quad7 13.3%, Liana 0.2%, Rav Palm5 0.4%
Overall orientation: A 46.7%, B 38.7%, C 14.1%
Total activity budget: Call 0.3%, Eat flowers 1.1%, Eat leaves 41.0%, Eat seeds 3.4%, Eat young leaves 8.3%
Total tree height: B 0.2%, C 1.2%, D 1.6%, E 4.2%, F 32.3%, G 25.2%, H 34.8%, I 0.1%

The range of indri group 14 was relatively small, located in the eastern section of the research area nested between indri groups 40 and 55 with some overlap with *Eulemur* group 34. The behavioral and movement data collected from this group was primarily based on observations made of the radio-collared adult female and her nearest neighbor (Figure 6.11). The indri in this group spent more than half of their time feeding (Figure 6.11).

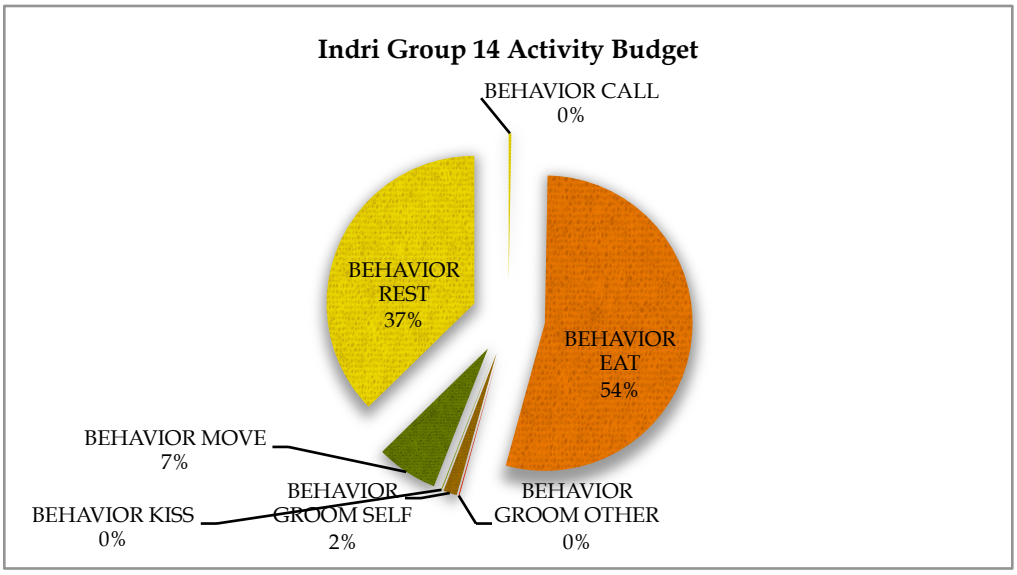


Figure 6.11 Indri Group 14 activity budget

FEEDING BEHAVIORS BY INDRI GROUP 14

Types of foods consumed by indri group 14

Out of the total amount of time spent engaged in feeding behaviors indri spent the most time feeding on leaves (76.3%) (Table 6.140).

Table 6.140 Foods consumed by Indri group 14

Food (N=544)	Total Count	Percentage
Flowers	11	2.0%
Mature Leaves	415	76.3%
Seeds	34	6.3%
Young Leaves	84	15.4%

Postures used for the consumption of different foods by indri group 14

The indri in group 14 displayed a variety of different postures for the consumption of different food items (Table 6.141). The most common posture for eating was a sit (47.2%) followed by a sit extend, postures where the majority of leaves were consumed (Table 6.141). Young leaf foraging primarily occurred in suspensory or vertical cling postures.

Table 6.141 Postures used for food consumption by Indri group 14

Posture (N=544)	Total Count	Percentage	Food eaten in position	Percentage
Recline	26	4.8%	EL, ES	92.3%, 7.7%
Sit Extend	172	31.6%	EFL, EL, ES, EYL	1.2%, 63.4%, 5.8%, 29.7%
Sit	257	47.2%	EFL, EL, ES, EYL	3.5%, 87.2%, 8.6%, 0.8%
Suspend	19	3.5%	EL, EYL	47.4%, 52.6%
Vertical Cling	70	12.9%	EL, EYL	70%, 30%

Size of substrate used by indri group 14 while feeding

Indri in group 14 used medium sized substrates for feeding behaviors (73.0%) and rarely used very small or large substrates (Table 6.142).

Table 6.142 Size of substrate used for food consumption by Indri group 14

Size of Substrate Used in Feeding	Count	Percentage of Use
Very Small (<1cm)	4	0.7%
Small (1-5 cm)	131	24.1%
Medium (6-10cm)	397	73.0%
Large (11-15 cm)	12	2.2%

Height of substrate used by indri group 14 while feeding

Indri group 14 fed within a wide height range but a higher frequency occurred at the heights of 9 to 10 meters (25.6%) and 12 to 13 meters (31.1%). A majority of the mature leaves were consumed higher in the canopy between the heights of 12 and 13 meters (38.1%), whereas most of the young leaves were consumed between the heights of 6 and 10 meters (90.5%) (Table 6.143).

Table 6.143 Height of substrate used for food consumption by Indri group 14

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	1	0.2%
B (2-3 m)	2	0.4%
C (4-5 m)	10	1.8%
D (6 m)	34	6.3%
E (7-8 m)	95	17.5%
F (9-10 m)	139	25.6%
G 11 (m)	94	17.3%
H (12-13 m)	169	31.1%
Total	544	100%

Orientation of substrate used by indri group 14 while feeding

Indri in group 14 focused on horizontal substrates (51.8%) as well as oblique substrates (39.2%) for feeding behaviors with much less focus on vertical supports. The food consumed with this limited vertical support use included young and mature leaves. The indri consumed the highest percentage of mature leaves and young leaves on horizontal supports (Table 6.144), whereas seeds and flowers were focused on with the use of oblique substrates (Table 6.144).

Table 6.144 Orientations of substrates used for food consumption by Indri group 14

Food	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%	TOTAL
Flowers	0	0%	11	100%	0	0%	11
Mature Leaves	230	55.4%	155	37.3%	30	7.2%	415
Seeds	12	35.3%	22	64.7%	0	0%	34
Young leaves	40	47.6%	25	29.8%	19	22.6%	84

Use of different tree quadrants while feeding by indri group 14

The indri in group 14 used a variety of different quadrants for feeding (Table 6.145) with a focus on quadrants 4 (27.5%), 5 (20%), and 6 (20%) for a majority of the leaf consumption. Most of the young leaves were consumed in quadrant 4 (42.9%).

Table 6.145 Quadrant used for food consumption by Indri group 14

Quadrant	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7
Flowers	0	0	0	9	0	2	0
Mature Leaves	46	32	30	114	82	81	30
Seeds	21	8	0	0	1	4	0
Young Leaves	0	0	7	36	19	19	3
Total	67	40	37	159	102	106	33

Foods consumed in different levels of canopy/vegetation connectivity by indri group 50

Indri group 50 frequently engaged in feeding behaviors in areas with small gaps in the canopy/vegetation (43.4%), but also foraged in areas with connected canopy/vegetation (27.4%) and medium-gapped (25.9%) canopy/vegetation (Table 6.146).

Table 6.146 Canopy/vegetation distances and foods consumed by Indri group 14

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium	Total
Eat Flowers	2	9	0	0	0	11
Eat Matures Leaves	94	0	173	7	141	415
Eat Seeds	0	0	34	0	0	34
Eat Young Leaves	53	2	29	0	0	84
Total	149	11	236	7	141	544

LOCOMOTION BY INDRI GROUP 14

Locomotor modes used by indri group 14

Overall, indri group 14 spent 7% out of their total activity budget moving. Indri in group 14 mainly moved by leaping varying distances. One (30.9%), two (26.5%), and three (25.0%) meter leaps were used relatively equal amounts of time (Table 6.147).

Table 6.147 Locomotor modes used by Indri group 14

Locomotor Modes (N=68)	Total Count	Percentage
Climb	4	6.0%
L<1	3	4.4%
L1	21	30.9%
L2	18	26.5%
L3	17	25%
L4	4	6.0%
Vertical Bound	1	1.5%
Total	68	100%

Size of substrate used for locomotion by indri group 14

Size of substrate affects movement (K-S, D_{MAX}=0.18, $p<0.05$). Indri group 14 focused more than half of their movement on medium substrates (61.8%) and the other half on small (22.1%) and large (16.8%) substrates (Table 6.148). Indri used a variety of different distance leaps and size of substrates for landing supports (Table 6.149).

Table 6.148 Different sized substrates used for movement by Indri group

Size of Substrate	Small	Medium	Large
Move	15	42	11

Table 6.149 Size of substrate and locomotor modes used by Indri group 14

Size of Substrate	Small	Medium	Large	Total
Climb	0	3	1	4
L<1	1	2	0	2
L1	6	12	3	20
L2	4	12	2	18
L3	3	10	4	17
L4	1	3	0	4
Vertical Bound	0	0	1	1
Total	15	42	11	68

Heights used by indri group 14 for locomotion

Height of substrate affects movement (K-S, D_{MAX}=0.26, p<0.01). Indri group 14 frequently moved at a height of 9 to 10 meters (35.3%) and 11 meters (20.6%) (Table 6.150). The indri used different distance leaps at this range of heights (Table 6.51).

Table 6.150 Different heights used for movement by Indri group 14

Height of Substrate	A	B	C	D	E	F	G	H
Move	2	2	4	9	10	24	14	3

Table 6.151 Heights of substrate and locomotor modes used by Indri group 14

Height of Substrate	A	B	C	D	E	F	G	H	TOTAL
Climb	0	0	1	0	0	1	1	1	4
L<1	0	0	1	0	0	1	1	0	3
L1	1	2	1	4	5	5	2	1	21
L2	0	0	0	2	1	10	4	1	18
L3	0	0	1	3	3	6	4	0	17
L4	1	0	0	0	1	1	1	0	4
Vertical Bound	0	0	0	0	0	0	1	0	1
Total	2	2	4	9	10	24	14	3	68

Substrate orientations used for different locomotor modes by indri group 14

Orientation of substrate influences indri movement (χ^2=40, df=2, p<0.001). Indri used vertical substrates 64.7% of the time with less focus on oblique, and hardly any time was given to horizontal substrates (Table 6.152).

Table 6.152 Locomotor modes used on varying oriented substrates by Indri group 14

Orientation	Horizontal	Oblique	Vertical
Climb	0	1	3
L<1	1	1	1
L1	1	7	13
L2	1	3	14
L3	0	8	9
L4	0	1	3
Vertical Bound	0	0	1
Total	3	21	44

Quadrant use for movement by indri group 14

Indri movement is influenced by tree quadrant (χ^2=163, df=6, p<0.001). Indri group 14 occupied quadrant 7 66.2% of the time for movement, mainly using one to three meter leaps (Table 6.153).

Table 6.153 Movement in varying quadrants used by Indri group 14

Quadrant	1	2	3	4	5	6	7	Liana	Rav Palm5
Move (N)	0	1	1	3	3	12	45	1	2

Canopy/vegetation connectivity and locomotor modes by indri group 14

The level of canopy/vegetation connectivity affects indri movement (K-S, D_{MAX}=0.21, p<0.01). Indri 14 used areas of connected canopy/vegetation 36.8% of the time with more focus on areas with small/medium gaps (50%). Although rare, there also was some movement through areas with medium/large and large gaps (Table 6.154). The level of canopy/vegetation connectivity also affected the locomotor mode used to negotiate the different forest types

(χ^2=11.13, df=2, p<0.01). In areas of connected canopy/vegetation 56.0% of the leaps were one meter (Table 6.155). In small/medium-gapped areas the focus was on two (32.4%) and three (40.2%) meter leaps and less so on one meter (14.7%) leaps. Between-substrate movement was more common (86.8%), using a variety of different distance leaps (Figure 6.12). Within-substrate movement mainly consisted of climbing (Figure 6.12).

Table 6.154 Canopy/vegetation connectedness used for movement by Indri group 14

Distance b/n Canopy	Connected	Small	Small/Medium	Medium	Medium/Large	Large
Move	25	0	34	0	8	1

Table 6.155 Canopy/vegetation connectedness and locomotor modes by Indri group 14

Distance b/n Canopy	Connected	Small/Medium	Medium/Large	Large	Total
Climb	1	1	2	0	4
L<1	1	2	0	0	3
L1	14	5	1	0	21
L2	5	11	2	0	18
L3	2	13	2	0	17
L4	2	2	0	1	4
Vertical Bound	0	0	1	0	1
Total	25	34	8	1	68

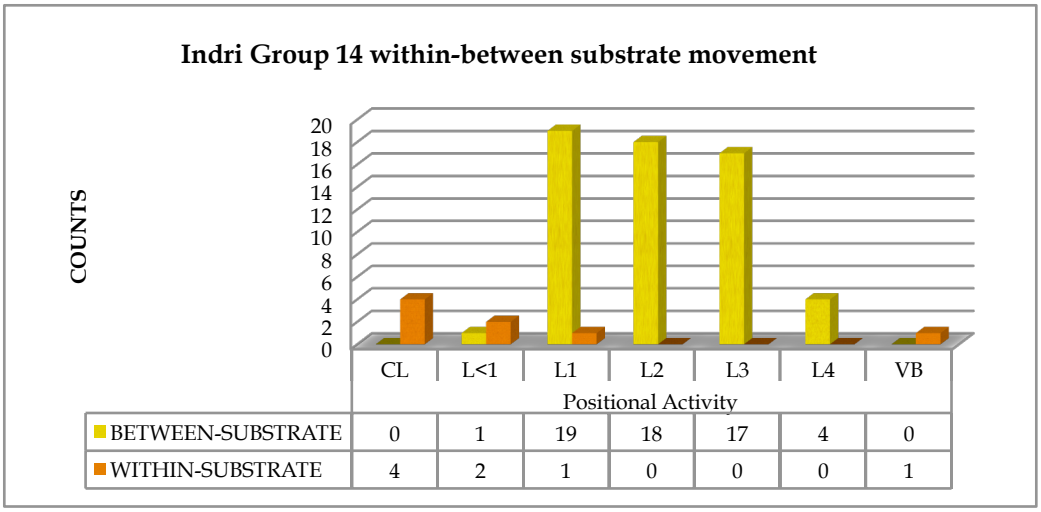


Figure 6.12 Indri group 14 within-between substrate movement

RESTING BEHAVIORS BY INDRI GROUP 14

Postures used for resting by indri group 14

Indri in group 14 commonly rested in sit (40.7%) and sit-extend (32.7%) postures (Table 6.156).

Table 6.156 Postural modes used while resting by Indri group 14

Postural Modes for Rest (N=376)	Total Count	Percentage
Recline	3	0.8%
Sit-Extend	123	32.7%
Sit	153	40.7%
VC	97	25.8%

Size of substrate used for resting by indri group 14

Indri resting behaviors are influenced by size of substrate (K-S, D_{MAX}=0.22, $p<0.01$). Indri group 14 used medium substrates for resting 77.7% of the time with much less focus on small or large substrates (Table 6.157).

Table 6.157 Different sized substrates used for resting behaviors by Indri group 14

Size of Substrate Resting	Total Count	Percentage
Small (1-5 cm)	40	10.6%
Medium (6-10 cm)	292	77.7%
Large (11-15 cm)	44	11.7%
Total	376	100%

Size of substrate used for different resting postural modes by indri group14

All of the postures used for resting occurred mainly on medium substrates (Table 6.158). Less time was devoted to the use of the other substrate sizes, but the indri were still capable of using these substrates on occasion.

Table 6.158 Different sized substrates used for resting postures by Indri group 14

Size of Substrate	Small	%	Medium	%	Large	%	Total
Recline	0	0%	3	100%	0	0%	3
Sit Extend	25	20.3%	96	78.0%	2	1.6%	123
Sit	4	2.6%	141	92.2%	8	5.3%	153
Vertical Cling	11	11.3%	52	53.6%	34	35.1%	97
Total	40		292		44		376

Substrate orientation used for resting by indri group 14

Indri resting behaviors are influenced by orientation of substrate (χ^2=75, df=2, p<0.001). Indri in group 14 rested relatively equal amounts of time on horizontal (46.3%) and oblique (41.2%) substrates (Table 6.159). As the most common postures, most of the sit-extend (55.3%) and sit (66.7%) postures occurred on horizontal substrates. Vertical-clinging while resting occurred on oblique (53.6%) and vertical substrates (45.4%).

Table 6.159 Different orientations used for resting behaviors by Indri group 14

Horizontal Count	%	Oblique Count	%	Vertical Count	%	Total
174	46.3%	155	41.2%	47	12.5%	376

Height of substrate and resting behavior by indri group 14

Indri resting behaviors are influenced by substrate height (K-S, D_{MAX}=0.36, p<0.01). Indri in group 14 rested at heights ranging from 1 meter to 13 meters but the most frequent height for rest for more extensive time periods was 9 to 10 meters (41.8%) (Table 6.160).

Table 6.160 Height of substrate used while resting by Indri group 14

Height of Substrate	A	B	C	D	E	F	G	H
Rest	3	6	21	21	75	157	29	64

Quadrant use and resting behavior by indri group 14

Indri have a preference for certain quadrants for rest (χ^2=188, df=6, p<0.001). The most frequent quadrant indri group 14 rested in was quadrant 6 (31.4%). The indri used all of the quadrants in some capacity except for quadrant 1, where no resting was observed (Table 6.161).

Table 6.161 Different quadrants used for resting by Indri group 14

Quadrant	1	2	3	4	5	6	7	Liana	Rav Palm5
Rest	0	19	25	71	86	118	54	1	2

Canopy/vegetation connectivity and resting behaviors by indri group 14

The level of canopy/vegetation connectivity affects resting behaviors (K-S, D_{MAX}=0.16, p<0.01). Indri group 14 rested primarily in areas with connection (27.9%) or small gaps (53.7%) in the canopy/vegetation (Table 6.162).

Table 6.162 Different canopy/vegetation distances used for rest by Indri group 14

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	105	2	202	4	63

INDRI GROUP 14 SUBSTRATE COMBINATIONS AND KEYSTONE STRUCTURES

Substrate Combinations

Orientation of substrate and quadrant use by indri group 14

Indri group 14 used horizontal substrates more frequently in quadrants 1, 2, and 5. The use of oblique substrates was more prominent in quadrants 3, 4, 6, and 7. The use of vertical substrates mainly occurred in quadrant 7 (Table 6.163).

Table 6.163 Quadrant and orientation used by Indri group 14

Quadrant	Horizontal	Oblique	Vertical
1	55	12	0
2	38	22	0
3	23	40	0
4	81	138	15
5	165	26	5
6	107	132	8
7	2	22	111
Liana	2	0	0
Rav Palm 5	0	0	4

Height of substrate and quadrant use by indri group 14

When indri were lower in the canopy (under 6 meters) they mainly used quadrant 7 (Table 6.164). At a height of 6 to 8 meters the indri frequently used quadrant 6. At a height of 9 to 10 meters the indri occupied quadrant 5. Quadrants 5 and 6 were mainly used at a height of 11 meters and quadrant 4 was mainly used at the tallest height of 12 to 13 meters.

Table 6.164 Height of substrate and quadrant use by Indri group 14

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Liana	Rav Palm5
A	0	0	0	0	0	0	6	0	0
B	0	0	0	1	0	0	9	0	0
C	0	0	0	1	3	13	18	0	0
D	0	0	0	11	5	33	15	0	0
E	0	0	0	53	19	71	38	0	2
F	0	19	16	70	108	76	39	2	2
G	21	21	0	14	36	40	9	0	0
H	46	20	47	84	25	14	1	0	0

Total tree height and height of substrate used by indri group 14

Unlike the previous two indri groups, indri in group 14 tended to focus their activities in the taller heights of the tree regardless of crown volume size and shape (Table 6.165).

Table 6.165 Height of substrate and height of tree used by Indri group 14

Height of tree	B	C	D	E	F	G	H	I
Height of Substrate								
A	1	4	0	0	0	0	1	0
B	1	8	0	0	1	0	0	0
C	0	0	5	13	8	9	0	0
D	0	0	11	0	48	4	1	0
E	0	0	0	30	103	50	0	0
F	0	0	0	0	167	134	31	0
G	0	0	0	0	0	58	83	0
H	0	0	0	0	0	0	236	1

Keystone Structures

The indri used keystone structures for resting, moving, and feeding. These substrates are presented in Table 6.166. A majority of the keystone structures for the indri were feeding trees.

Table 6.166 Keystone structures for Indri group 14

Malagasy Tree	Dbh (cm)	Height (m)	Activity	GPS
Antafonona	27.5	10.8	Feeding leaves	(0309593, 8018684)
Antaivaratra	30	10.2	Resting	(0309628, 8018600)
Mampay	19.6	10.6	Feeding leaves	(0309807, 8018607)
Vongo	6.5	6.3	Feeding leaves	(0309583, 8018502)
Azinina	9.1	7.8	Feeding leaves	(0309622, 8018449)
Tavolo	20.1	10.9	Feeding leaves/Moving	(0309534, 8018407)
Vintanona	48.2	11.9	Feeding leaves	(0309534, 8018407)

INDRI 14 NEAREST NEIGHBOR

Identity of nearest neighbor

The juvenile was nearest neighbor to the focal female 60.2% of the time whereas the male was nearest neighbor only 14.5%. The focal female traveled, rested, and fed on her own for full

days or portions of the day where she would be more than 20 meters away from the other group members (Table 6.167).

Table 6.167 Nearest neighbor of focal female in Indri group 14

Nearest Neighbor	Focal Female
Juvenile	606
Juvenile/Male	21
Male	88
>20 meters	291

Distance of nearest neighbor

When the juvenile was the nearest neighbor to the female she ranged from being in contact up to 15 meters away (Table 6.167). The most common distances were one meter (29.3%) and three meters (25.6%). When the male was nearest neighbor, he ranged from being in contact to 6 meters away. The most common distances included two meters (32.2%) and three meters (43.7%).

INDRI GROUP 14 SUMMARY STATEMENT

Microhabitat features influenced indri group 14's movement, feeding, and resting behaviors. These paragraphs highlight those substrates that indri group 14 utilized at a higher frequency than others, but as noted in the preceding sections, the indri in this group were capable of utilizing a wide range of different heights and substrates for resting, eating, and moving. In summary, indri group 14 used medium substrates at the heights of 9 to 10 meters in quadrants 4 and 6 on horizontal branches. A majority of their time was spent feeding and resting with little time devoted to moving. This indri group spent the most time feeding relative to their other activities. The other indri groups also spent ample time feeding, but the time spent feeding was comparable to the time resting. The adult female in group 14 was the largest female (8.4 kg) compared to the other indri or sifaka groups in this research perhaps driving the higher feeding percentage due to the female requiring more food on a daily basis. The total tree height mainly used by indri group 14 ranged from 9 to 10 meters and 12 to 13 meters. During each all day follow the substrates that this group

used were flagged and identified when possible. A list of the trees used for resting, moving, and feeding is included in the appendix. Indri group 14 used a variety of tree species but showed a heightened preference for some trees more so than others. These keystone trees were important for resting, moving, and feeding behaviors and were consistently monopolized. For feeding behaviors group 14 focused on rara leaves (N=8), mampay leaves (N=6), azinina leaves (N=7), and ate flowers from antafara and vintanona trees. Overall, the most common trees group 50 used for all behaviors included rara (N=8), azinina (N=10), mampay (N=8), tavolo fotsy (N=6), and antafonona (N=6).

Mature leaves were the main food type consumed by indri group 14 in a sit posture on medium horizontal substrates at a height of 9 to 10 or 12 to 13 meters. The indri primarily fed in quadrants 4, 5, and 6 in forested areas with small gaps in the canopy/vegetation. Unlike the indri groups 40 and 50, indri group 14 focused their activities in the taller heights of the tree regardless of crown volume size and shape.

Indri in group 14 only moved 7% of the time out of their total activity budget. The movement throughout the forest consisted mainly of between-substrate movement via equal proportions of one, two, and three meter leaps. The indri moved on medium vertical substrates at a height of 9 to 10 meters in quadrant 7 through areas with small/medium gaps in the canopy/vegetation. The indri focused more on two and three meter leaps in areas with larger gaps and used smaller distance leaps in areas with more connectivity. The exceptions were in the medium/large category where the indri did not use four meter leaps and the large-gapped category where the indri did use four meter leaps.

Indri group 14 used a variety of different quadrant and orientation of substrate combinations with no central focus. Oblique and horizontal oriented substrates were used in the peripheral space of the tree as well as space closer to the trunk and core of the tree. The indri groups also used multiple quadrants at different heights with the only central pattern consisting of

the indri using quadrant 7 at lower heights. Additionally, the indri exploited numerous height of substrate and height of tree combinations. Group 14 leaned more towards the taller heights of the tree regardless of the crown volume and shape.

The indri rested in sit or sit-extend postures on medium substrates on horizontal or oblique substrates at a height of 9 to 10 meters mainly in quadrant 6. The indri rested in areas that contained small gaps in the canopy/vegetation.

The adult female was more than 20 meters away from the other group members 30% of the time. She traveled, rested, and fed on her own for full days or partial days only to reconvene with the other group members later in the evening. When there was a nearest neighbor it was often the juvenile and less so the adult male.

Indri group 14 appeared to have a heightened preference for certain micro-habitat features. Although the indri did not demonstrate much variation in the use of different habitat types within their small range (discussed more in Section II).

Subsection 6.7
INDRI GROUP 45

INDRI GROUP 45: Group composition consisted of one adult female (Sue) and one adult male (Howard).
Female radio collar. 6.8 kg, body length 51.0 cm, tail length 4.3 cm
Male purple collar. 6.0 kg, body length 47.0 cm, tail length 5.0 cm.

Overall size of substrate: A 0.9%, B 19.2%, C 62.1%, D 17.8%
Overall height of substrate: A 2.4%, B 6.5%, C 8.7%, D 3.5%, E 15.9%, F 21.9%, G 28.0%, H 11.0%, I 2.1%
Overall quadrant: Quad1 7.2%, Quad2 7.2%, Quad3 5.6%, Quad4 21.3%, Quad5 9.2%, Quad6 34.0%, Quad7 15.3%, Liana 0.2%
Overall orientation: A 34.2%, B 48.5%, C 17.3%
Total activity budget: Eat leaf base 0.1%, Eat bark 4.2%, Eat flowers 3.8%, Eat leaves 27.0%, Eat young leaves 6.5%, Groom other 0.1%, Groom-self 1.9%, Kiss 0.1%, Move 5.1%, Rest 51.5%
Total tree height: A 0.1%, B 0.1%, C 4.5%, D 4.9%, E 4.6%, F 21.1%, G 36.7%, H 25.7%, I 2.3%.

The range of indri group 45 was located in the western portion of the research area. Despite the small group size, Sue and Howard went their separate ways for partial days or more often full days 50% of the time. Group 45 was the least cohesive of all the indri groups. Because the group split so frequently the behavioral and movement data collected from this group was primarily on observations made of the radio-collared female.

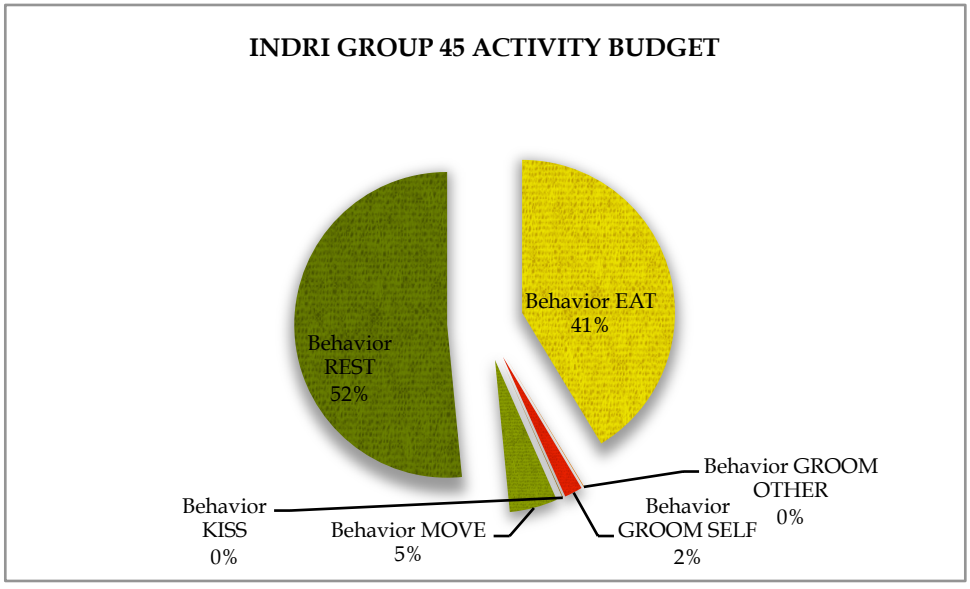


Figure 6.13 Indri Group 45 activity budget

FEEDING BEHAVIORS BY INDRI GROUP 45

Types of foods consumed by indri group 45

Out of the total amount of time expended in feeding behavior, indri spent the most time feeding on leaves (65.0%) (Table 6.168). An interesting component of the diet of group 45 was tree bark. Along with indri group 55, Sue and Howard were the only other indri group observed to eat bark. Complete branches of trees within the home range of group 45 were missing bark where the indri had gouged it out with their tooth-comb and then consumed it.

Table 6.168 Foods consumed by indri group 45

Food (N=628)	Total Count	Percentage
Tree Bark	64	10.2%
Flowers	57	9.1%
Mature Leaves	408	65.0%
Leaf Base	1	0.2%
Young Leaves	98	15.6%

Postures used for the consumption of different foods by indri group 45

The indri in group 45 displayed a variety of different postures for the consumption of different food items (Table 6.169). The most frequented posture was a sit (57.8%), where a majority of the leaves were consumed. Bark consumption was conducted in a variety of postures with a focus on vertical-clinging (19.4%) and reclining (13.8%), whereas a sit-extend posture was primarily used for flower consumption (19.2%) (Table 6.169).

Table 6.169 Postures used for foods consumed by indri group 45

Posture (N=628)	Total Count	Percentage	Food eaten in posture	Percentage
Recline	29	4.6%	EB[17], EFL, EL, EYL	13.8%, 6.9%, 55.2%, 24.1%
Sit Extend	125	19.9%	EB, EFL, EL, EYL	12.0%, 19.2%, 50.4%, 18.4%
Sit	363	57.8%	EB, EFL, EL, EYL, ELB	6.9%, 7.7%, 76.3%, 8.8%, 0.3%
Suspend	13	2.1%	EB, EL, EYL	7.7%, 76.9%, 15.4%
Vertical Cling	98	15.6%	EB, EFL, EL, EYL	19.4%, 3.1%, 42.9%, 34.7%

Size of substrate use by indri group 45 while feeding

Indri in group 45 used medium sized substrates (62.1%) for feeding behaviors (Table 6.170) and rarely used very small (1.4%) or large (6.8%) sized substrates.

Table 6.170 Size of substrate used for food consumption by indri group 45

Size of Substrate Used in Feeding	Count	Percentage of Use
Very Small (<1 cm)	9	1.4%
Small (1-5 cm)	186	29.6%
Medium (6-10 cm)	390	62.1%
Large (11-15 cm)	43	6.8%

Height of substrate used by indri group 45 while feeding

Indri group 45 fed within a wide height range, but a higher percentage of time was spent at the heights of 11 meters (27.5%) and 12 to 13 meters (19.3%) (Table 6.171). More than half of the bark consumption (57.8%) was completed at the lower heights of two to three meters. Young leaves were also mainly (30.6%) eaten lower in the canopy between the heights of four and five meters. In contrast, the indri focused on eating mature leaves higher in the canopy (77.2%) between the heights of 9 and 13 meters.

[17] EB=eat bark, ELB=eat leaf base

Table 6.171 Height of substrate used for food consumption by indri group 45

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	24	3.8%
B (2-3 m)	52	8.3%
C (4-5 m)	60	10.0%
D (6 m)	26	4.1%
E (7-8 m)	31	4.9%
F (9-10 m)	109	17.4%
G 11 (m)	173	27.5%
H (12-13 m)	121	19.3%
I (14-15 M)	32	5.1%
Total	628	100%

Orientation of substrate used by indri group 45 while feeding

Indri group 45 focused on horizontal (46.3%) and oblique (40.3%) branches for a majority of their feeding behaviors with less emphasis on vertical supports (Table 6.172). The foods consumed with the limited vertical support use included bark and young leaves (Table 6.172). The highest percentage of flowers was consumed on horizontal substrates, as was that of young leaves. Mature leaves were consumed relatively equal proportions of time on both horizontal and oblique substrates.

Table 6.172 Orientation of substrate used for food consumption by indri group 45

Food	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%	Total
Tree Bark	9	14.1%	41	65.1%	14	21.9%	64
Flowers	46	80.7%	8	14.0%	3	5.3%	57
Mature Leaves	194	47.5%	177	43.4%	37	9.1%	408
Leaf Base	1	100%	0	0%	0	0%	1
Young Leaves	41	39.0%	27	25.7%	37	35.2%	105
TOTAL	291		253		84		628

Use of different tree quadrants while feeding by indri group 45

The indri in group 45 used a variety of quadrants for feeding (Table 6.173) with a main focus on quadrant 4 (30.4%). Out of all of the quadrants, mature leaves were mainly consumed in

quadrant 4 (35.0%), whereas many of the young leaves were consumed in quadrants 6 and 7. The indri also used quadrants 4 and 6 for the consumption of bark (Table 6.173).

Table 6.173 Quadrant used for food consumption by indri group 45

Quadrant	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	QuadLiana
Tree Bark	0	7	5	23	0	18	11	0
Flowers	22	3	0	6	26	0	0	0
Mature Leaves	62	39	51	143	36	52	24	1
Leaf Base	0	0	0	0	0	1	0	0
Young Leaves	0	10	0	19	13	22	34	0
Total	84	59	56	191	75	93	69	1

Foods consumed in different levels of canopy/vegetation connectivity by indri group 45

Indri in group 45 frequently engaged in feeding behaviors in areas with connected (31.6%), small-gapped (20.6%), and medium-gapped (28.7%) canopy/vegetation (Table 6.174).

Table 6.174 Different canopy/vegetation distances and foods consumed by indri group 45

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Tree Bark	53	0	0	9	2
Flowers	0	26	31	0	0
Mature Leaves	59	32	97	44	176
Leaf Base	0	0	1	0	0
Young Leaves	84	7	7	0	0
Total	196	65	128	53	178

LOCOMOTION BY INDRI GROUP 45

Locomotor modes used by indri group 45

Indri group 45 moved by one (42.9%), two (42.9%), and three (13.0%) meters leaps throughout the forest (Table 6.175).

Table 6.175 Locomotor modes by indri group 45

Locomotor Mode (N=77)	Total Count	Percentage
L1	33	42.9%
L2	33	42.9%
L3	10	13.0%
Vertical Bound	1	1.3%
TOTAL	77	100%

Size of substrate used for locomotion by indri group 45

Size of substrate does not affect movement (K-S, D_{MAX}=0.14, p>0.05). Indri group 45 used a variety of substrates for movement. Indri group 45 concentrated more than half of their movement (59.7%) on medium sized substrates (Table 6.176) and the other half on small (20.8%) and large (19.5%) substrates. Indri in group 45 applied one meter leaps more to small and medium substrates, whereas two and three meter leaps were applied to medium and large substrates (Table 6.177).

Table 6.176 Different sized of substrates for movement by indri group 45

Size of Substrate	Small	Medium	Large
Move	16	46	15

Table 6.177 Different sized substrates and locomotor modes used by indri group 45

Size of Substrate	Small	Medium	Large	Total
L1	10	19	4	33
L2	5	22	6	33
L3	1	4	5	10
Vertical Bound	0	1	0	1
Total	16	46	15	77

Heights used by indri group 45 for locomotion

The height of substrate affects movement for indri group 45 (K-S, D_{MAX}=0.19, $p<0.05$). Indri group 45 used a wide range of low and high heights for movement, with more focus towards heights above 7 meters. The indri spent fairly equal proportions of time moving at the height of 4 to 5 meters (16.9%), 7 to 8 meters (20.8%), 9 to 10 meters (16.9%), and 11 meters (23.4%) (Table 6.178). Indri used a variety of different distance leaps at a range of heights with no tendency for specific distances at specific heights (Table 6.179).

Table 6.178 Different heights used for movement by indri group 45

Height of Substrate	A	B	C	D	E	F	G
Move	5	5	13	7	16	13	18

Table 6.179 Height of substrate and locomotor modes used by indri group 45

Height of substrate	A	B	C	D	E	F	G	TOTAL
L1	3	1	9	4	4	2	10	33
L2	1	3	3	3	11	7	5	33
L3	1	1	1	0	0	4	3	10
Vertical Bound	0	0	0	0	1	0	0	1
TOTAL	5	5	13	7	16	13	18	77

Substrate orientations used for different locomotor modes by indri group 45

Orientation of substrate influences indri movement (χ^2=45, df=2, $p<0.001$). Indri centered their efforts on vertical substrates for movement (Table 6.180). All of the distances used for leaping were focused on vertical substrates although horizontal and oblique substrates were also occasionally used.

Table 6.180 Locomotor modes used on varying oriented substrates by indri group 45

Orientation	Horizontal	Oblique	Vertical
L1	3	10	20
L2	1	7	25
L3	1	3	6
Vertical Bound	0	0	1
Total	5	20	52

Quadrant use for movement by indri group 45

Indri moving behavior is influenced by tree quadrant (χ^2=203, df=7, p<0.001). Indri group 45 occupied quadrant 7 59.2% of the time for movement with the primary use of one and two meter leaps (Table 6.181). The indri also used quadrant 6 for movement mainly through one meter leaps.

Table 6.181 Quadrant used for movement by indri group 45

Quadrant	1	2	3	4	5	6	7	Liana
Move	1	3	1	1	4	21	45	1

Canopy/vegetation connectivity and locomotor modes by indri group 45

The level of canopy/vegetation connectedness affects movement (K-S, D_{MAX}=0.24, p<0.01). Indri group 45 mainly moved through connected canopy/vegetation areas (49.4%) with the least amount of movement through areas with medium gaps (10.4%) (Table 6.182). The level of connectivity does not affect locomotor mode (χ^2=3, df=2, p>0.05). The indri used their full range of leaping distances for all levels of connectivity. For example, in areas with connected canopy the indri moved by one meter leaps and continued this distance of leaps even in areas with larger gaps (Table 6.183). Almost all of the movement recorded for indri group 45 was between-substrate (95.0%) movement primarily consisting of one meter leaps (Figure 6.14).

Table 6.182 Levels of canopy/vegetation connectedness used for movement by indri group 45

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Move	38	10	21	0	8

Table 6.183 Levels of canopy/vegetation connectedness and locomotor modes by indri group 45

Distance b/n Canopy	Connected	Connected/Small	Small	Medium
L1	17	2	11	3
L2	17	6	6	4
L3	3	2	4	1
Vertical Bound	1	0	0	0
Total	38	10	21	8

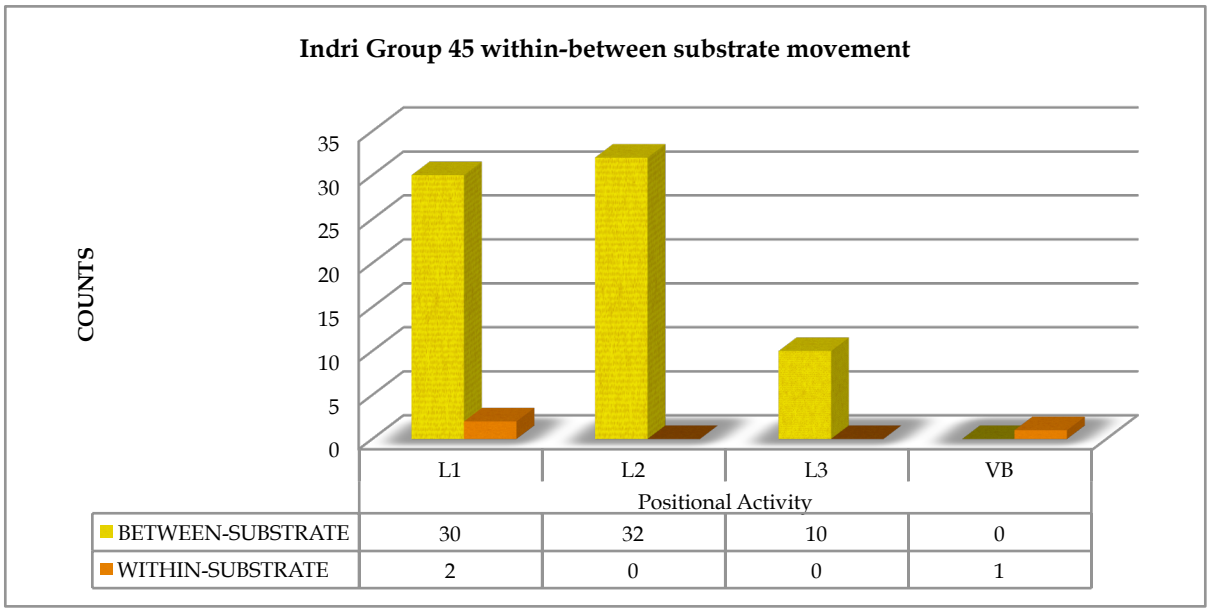


Figure 6.14 Indri group 45 within-between substrate movement

RESTING BEHAVIORS BY INDRI GROUP 45

Postures used for resting by indri group 45

Indri group 45 spent about half of their time in a sit posture for rest while the other half was divided evenly between a sit-extend posture and a vertical-cling posture (Table 6.184).

Table 6.184 Postural modes used while resting by indri group 45

Postural Modes for Rest (N=783)	Total Count	Percentage
Sit Extend	196	25.0%
Sit	386	49.3%
Vertical Cling	201	25.7%

Size of substrate used for resting by indri group 45

Indri resting behaviors are influenced by size of substrate (K-S, D_{MAX}=0.38, $p<0.01$). Indri group 45 used medium substrates for resting 62.6% of the time and large substrates 25.8% of the time with less focus on small or very small substrates (Table 6.185).

Table 6.185 Different sized substrates used for resting behaviors by indri group 45

Size of Substrate Resting	Total Count	Percentage
Very Small (<1 cm)	5	0.6%
Small (1-5 cm)	86	11.0%
Medium (6-10 cm)	490	62.6%
Large (11-15 cm)	202	25.8%
Total	783	100%

Size of substrate used for different resting postural modes by indri group 45

All the postures used for resting occurred mainly on medium substrates (Table 6.186). The only resting posture used on very-small substrates was a sit-extend (Table (6.186).

Table 6.186 Different sized substrates used for resting postures by indri group 45

Size of Substrate	Very Small	%	Small	%	Medium	%	Large	%	Total
Sit Extend	5	2.6%	30	15.3%	125	63.8%	36	18.4%	196
Sit	0	0%	36	9.3%	240	62.2%	110	28.5%	386
Vertical Cling	0	0%	20	10.0%	125	62.2%	56	28%	201
Total	5		86		490		202		

Substrate orientation used for resting by indri group 45

Indri resting behaviors are influenced by orientation of substrate (χ^2=217, df=2, p<0.001). The indri occupied oblique substrates 57.5% of their resting time (Table 6.187). Sit-extend (77.6%) and sit (57.9%), the most common resting postures, mainly occurred on oblique substrates. Vertical-clinging and resting occurred on vertical substrates and oblique substrates.

Table 6.187 Different orientations used for resting behaviors by indri group 45

Horizontal Count	%	Oblique Count	%	Vertical Count	%	Total
206	26.3%	450	57.5%	127	16.2%	783

Height of substrate and resting behavior by indri group 45

Indri resting behaviors are influenced by substrate height (K-S, D_{MAX}=0.44, p<0.01). Indri 45 used a wide range of heights for resting but centered their attention at the heights of 7 to 8 (14.6%) meters, 9 to 10 (15.6%) meters, and 11 (16.6%) meters (Table 6.188).

Table 6.188 Height of substrate used while resting by indri group 45

Height of Substrate	A	B	C	D	E	F	G	H
Rest	7	40	59	20	191	204	217	45

Quadrant use and resting behavior by indri group 45

Indri have a preference for certain quadrants for resting (χ^2=1155, df=7, p<0.001). Indri rested in quadrant 6 more than 50% of their time (Table 6.189).

Table 6.189 Different quadrants used for resting by indri group 45

Quadrant	1	2	3	4	5	6	7	Liana
Rest	25	43	28	125	50	393	118	1

Canopy/vegetation connectivity and resting behaviors by indri group 45

The level of canopy/vegetation connectivity affects resting (K-S, D_{MAX}=0.27, p<0.01). Indri group 45 frequently rested in areas with connected canopy/vegetation (43.9%) and small-gapped areas (29.2%) (Table 6.190).

Table 6.190 Distances in canopy connectivity used for resting behaviors by indri group 45

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	344	108	229	22	80

INDRI GROUP 45 SUBSTRATE COMBINATIONS AND KEYSTONE STRUCTURES

Substrate Combinations

Orientation of substrate and quadrant use by indri group 45

Indri group 45 used horizontal substrates more frequently in quadrants 1, 2, 3, and 5. In quadrant 4 the indri used horizontal and oblique substrates an equal amount of time. Indri used oblique substrates in quadrant 6 and vertical substrates were used in quadrant 7 (Table 6.191).

Table 6.191 Quadrant and orientation used by indri group 45

Quadrant	Horizontal	Oblique	Vertical
1	34	76	0
2	59	43	8
3	70	15	0
4	152	156	15
5	113	26	0
6	89	400	27
7	1	20	212
Liana	1	1	1

Height of substrate and quadrant use by indri group 45

When the indri were lower in the canopy they mainly used quadrants 6 and 7. Quadrant 6 was the primary quadrant used at a height of 7 to 8 meters. Quadrant 6 was also used at a height of 9 to meters along with quadrant 4. Quadrants 4 and 6 along with quadrant 5 were all frequently used at a height of 11 meters. At the height of 12 to 13 meters quadrant 1 was the main quadrant and at the tallest height of 14-15 meters, only quadrant 3 was occupied (Table 6.192).

Table 6.192 Height of substrate and quadrant used by indri group 45

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Liana
A						10	25	2
B				33		28	37	
C		7		6	1	50	67	1
D				13		9	31	
E	2	7	2	12	8	173	37	
F	1	27	39	102	10	124	30	
G	29	50		109	120	113	5	
H	78	19	12	48		9	1	
I			32					

Total tree height and height of substrate used by indri group 45

Indri group 45 used a wide range or height of substrate and height of tree combinations. The indri maximized the space available in the tree using lower heights all the way to the tallest heights in the canopy (Table 6.193).

Table 6.193 Height of substrate and total height of tree used by indri group 45

	Height of Tree								
Height of Substrate	A	B	C	D	E	F	G	H	I
A	2		13	1	12	9			
B		1	47	19	4	22	5		
C			8	28	23	41	27	4	1
D				19	15	18	1		
E				8	15	195	18	4	1
F					1	35	244	52	1
G							261	165	
H							1	166	
I									32

Keystone Structures

The indri frequently used space that was either closed or open showing variation in their use of different patch types. Much of their home range consisted of small streams in addition to encompassing part of the Ivoloina River that runs through BNR. The home range of indri group 45 also included 400 m^2 fields as well as smaller pockets of longoza. Long stretches of the forest utilized by the indri contained extensive growth of voapaka trees. Each of the trees grew in close proximity to the next leaving less than one meter space available between trees in some areas. The indri used important keystone structures in their environment for resting, feeding, and moving. These keystone structures are presented in Table 6.194. These keystone structures primarily consisted of feeding trees.

Table 6.194 Keystone structures used by indri group 45

Malagasy Tree	Dbh (cm)	Height (m)	Activity	GPS
Tsimamasatsokina	5	3.8	Feeding leaves	(0310590, 8018396)
Rara	25.2	10.8	Feeding leaves	(0310544, 8018526)
Tavolo fotsy	9	10.1	Resting	(0310425, 8018627)
Voapaka beravina	52	10.4	Feeding leaves/Resting	(0310425, 8018627)
Zambo	30	10.9	Moving	(0310425, 8018627)
Antafonona	9	10.5	Feeding leaves, bark/ Resting	(0310390, 8018525)

INDRI 45 NEAREST NEIGHBOR

Identity of nearest neighbor

The only nearest neighbor to Sue was Howard, the only other member in the group (Table 6.195). Sue spent 50% of her time with Howard and the other half on her own.

Table 6.195 Nearest neighbor of indri group 45

Nearest Neighbor	Focal Female
Male	769
>20 meters	743

Distance to nearest neighbor

The 50% of the time that Sue was with Howard she was usually one to three meters away from him, although a broad range of distances was used (Table 6.196).

Table 6.196 Nearest neighbor distance of indri group 45

Distance	0	1	2	3	4	5	6	8	10	12	15	>20
Howard	64	110	235	160	60	30	32	26	46	4	1	743

Summary Statement Indri Group 45

Microhabitat influences indri group 45 resting, feeding, and moving behaviors. These paragraphs highlight those substrates that indri group 45 utilized at a higher frequency than others, but as noted in the preceding sections, the indri in this group were adept at utilizing a wide range of different heights and substrates for resting, eating, and moving. In summary, indri group 45 used medium substrates at the heights of 9 to 11 meters in quadrants 4 and 6 on oblique branches. A majority of their time was spent feeding and resting with little time devoted to moving. The total tree height mainly used by indri group 45 ranged from 11 to 13 meters. During each all day follow the substrates that this group used were flagged and identified when possible. The list of the trees used for resting, moving, and feeding is included in the appendix. Indri group 45 used a variety of tree species but showed a heightened preference for some trees. The indri used important keystone structures in their environment for resting, feeding, and moving. Some days Sue only foraged in two or three trees over the course of the entire day. For feeding behaviors group 45 focused on rara leaves (N=5) and tavolo fotsy leaves and bark (N=5). Overall, the most common trees group 45 used for all behaviors included rara (N=12), azinina (N=6), tavolo fotsy (N=10), voapaka keliravina (N=10), and zambo (N=6).

Out of the total amount of time expended towards feeding behaviors, the indri spent the most time feeding on mature leaves commonly in a sit posture on medium sized horizontal or oblique substrates between the heights of 11 and 13 meters. Indri group 45 mainly used quadrant 4 for feeding behaviors in areas with connected or small-gapped canopy/vegetation. Indri group 45 consumed bark from tavolo fotsy trees as a component of their diet. Group 45 and only one other indri group (Group 55) were observed to eat bark, although the consumption of bark was more prevalent in group 45 particularly with Sue.

Indri in group 45 focused their efforts towards one and two meter leaps for movement onto medium vertical substrates in quadrant 7. Indri in group 45 applied one meter leaps more so to

small and medium substrates whereas two and three meter leaps were applied to medium and large substrates. The indri used a wide range of different heights for movement with no real focal height. The indri did use the heights between 7 and 11 meters at a slightly higher frequency than the other lower heights. The indri mainly used between-substrate movement through areas of connected canopy/vegetation, using their full range of leaping distances.

Indri 45 used a sit posture for rest on medium oblique substrates between the heights of 7 to 11 meters in quadrant 6. The indri rested in areas of connected canopy/vegetation. The indri used a wide range of height of substrate and height of tree combinations, maximizing the available space in the entire tree by using lower heights in addition to the tallest heights in the canopy. Group 45 demonstrated more diversity in the orientation and quadrant used. For example, group 45 used horizontal substrates in central and peripheral quadrants of the canopy and also varied their use of different orientations even within the same quadrant.

The only nearest neighbor to Sue was Howard, the only other group member. Sue spent half of her time around Howard, usually within one to three meters, and the other half of her time was spent moving, resting, and feeding on her own. Sue and Howard had the least group cohesion of all the indri groups despite only having a group of two. In other groups it was often the juvenile that was the nearest neighbor. Perhaps the lack of juveniles in group 45 influenced social spacing. In other groups the focal animals spent time away from their group but not to the extent that Sue and Howard spent apart. Howard was observed to approach Sue on occasions, seeming to shorten the gap between them, only to be left in the tree alone as Sue moved trees or left the vicinity.

Group 45 was flexible in their ability to utilize a wide spectrum of different substrates, orientations, and heights for resting, feeding, and moving behaviors. The indri appeared to have a heightened preference for certain substrates but are also quick to make adjustments and use other forest elements.

Subsection 6.8
INDRI GROUP 55

INDRI GROUP 55: Group composition consisted of 1 adult female (Blue), 2 adult males, and 1 male juvenile (Fozzie).
Male radio collar (Kermit). 6.5 kg, body length 49 cm, tail 3.7 cm.
Female blue collar. 7.3 kg, body length 5.3 cm, tail length 5.3 cm.
Male pink collar (Pinky). 5.9 kg, body length 43.5 cm, tail 6 cm.
Juvenile. Not captured.

Overall size of substrate: B 19.9%, C 52.8%, D 27.3%
Overall height of substrate: A 0.7%, B 1.3%, C 2.9%, D 11.1%, E 13.1%, F 27.7%, G 25.7%, H 15.7%, I 1.8%
Overall quadrant: Quad1 7.8%, Quad2 12.0%, Quad3 8.4%, Quad4 19.3%, Quad5 9.6%, Quad6 28.0%, Quad7 13.9%, Knot 0.5%, Liana 0.2%, Palm leaf4 0.07%, Rav Palm 5 0.3%
Overall orientation: A 31.7%, B 55.3%, C 13.1%
Total activity budget: Eat bark 1.0%, Eat flowers 1.3%, Eat leaves 31.4%, Eat young leaves 7.8%, Groom-self 2.7%, Kiss 0.07%, Move 6.1%, Rest 49.6%
Total tree height: B 0.3%, C 0.5%, D 0.7%, E 7.9%, F 19.1%, G 37.7%, H 34.2%, I 4.6%

The behavioral and movement data collected from this group was primarily based on observations made of the radio-collared adult male and his nearest neighbor. The indri in this group spent half of their time resting, a comparable amount of time feeding (41%), and 6% of their time was devoted to moving (Figure 6.15).

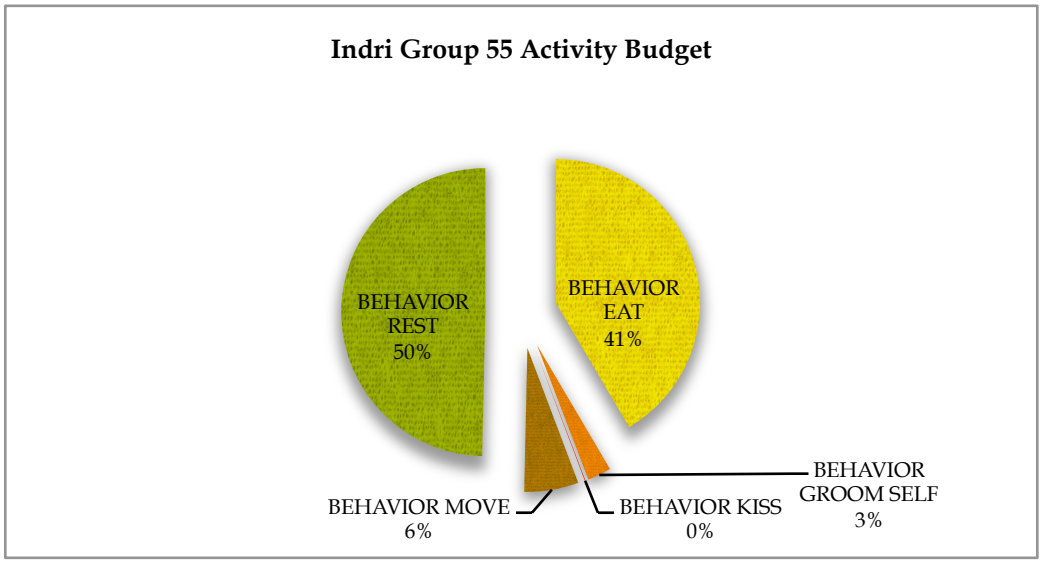


Figure 6.15 Indri Group 55 Activity Budget

FEEDING BEHAVIORS INDRI GROUP 55

Types of foods consumed by indri group 55

Out of the total amount of time applied towards feeding behaviors indri in group 55 spent over 75% of the time feeding on mature leaves (Table 6.197). Similar to group 45, as discussed in the previous section, group 55 consumed bark as a component of their overall diet, although to a lesser extent of what was observed of the indri in group 45.

Table 6.197 Foods consumed by indri group 55

Food (N=593)	Total Count	Percentage
Tree Bark	14	2.4%
Flowers	18	3.0%
Mature Leaves	449	75.7%
Young Leaves	112	18.9%

Postures used for the consumption of different foods by indri group 55

Indri group 55 used a variety of different postures for the consumption of different food items (Table 6.198). Feeding by the indri was in a sit posture over 50% of the time (Table 6.198) where all of the different types of foods eaten by indri group 55 were consumed albeit with varying percentages of time. Flowers, along with leaves, were mainly consumed using suspensory postures, whereas bark was eaten while in sit or sit-extend postures (Table 6.198). Mature and young leaves were consumed in all postures.

Table 6.198 Postures used for food consumption by indri group 55

Posture (N=593)	Total Count	Percentage	Food eaten in posture	Percentage
Recline	33	5.6%	EL	100%
Sit Extend	169	28.5%	EB, EL, EYL	3.0%, 64.5%, 32.5%
Sit	307	51.8%	EB, EFL, EL, EYL	2.9%, 5.5%, 82.7%, 8.8%
Suspend	12	2.0%	EFL, EL, EYL	8.3%, 75%, 16.7%
Vertical Cling	72	12.1%	EL, EYL	61.1%, 39.0%

Size of substrate used by indri group 55 while feeding

Indri in group 55 used medium substrates more than 50 percent of the time (Table 6.199). The indri also used small substrates (26.3%) more frequently than large substrates (15.3%).

Table 6.199 Size of substrate used for food consumption by indri group 55

Size of Substrate Used in Feeding	Count	Percentage of Use
Small (1-5 cm)	156	26.3%
Medium (6-10 cm)	346	58.3%
Large (11-15 cm)	91	15.3%

Height of substrate used by indri group 55 while feeding

Indri group 55 fed within a wide range of heights, but a higher percentage of time occurred at the heights of 9 to 10 (19.4%), 11 (31.2%), and 12 to 13 (20.9%), with the least amount of time occurring at the lowest heights of one to three meters (Table 6.200).

Table 6.200 Height of substrate used for food consumption by indri group 55

Height of Substrate Used in Feeding	Total Count	Percentage of Use
A (1 m)	7	1.2%
B (2-3 m)	5	0.8%
C (4-5 m)	8	1.3%
D (6 m)	67	11.3%
E (7-8 m)	65	11.0%
F (9-10 m)	115	19.4%
G 11 (m)	185	31.2%
H (12-13 m)	124	20.9%
I (14-15 m)	17	2.9%
Total	593	100%

Orientation of substrate used by indri group 55 while feeding

Indri used oblique substrates more frequently (51.8%) for feeding behaviors (Table 6.201), although horizontal (41.3%) and vertical (6.9%) were occupied as well (Table 6.200). All of the flowers were consumed on oblique substrates in addition to a higher percentage of mature leaves. Young leaves were eaten an equal percentage of time on both horizontal and oblique substrates (Table 6.201). The indri only ate tree bark on horizontal substrates.

Table 6.201 Orientation of substrate used for food consumption by indri group 55

Food	Horizontal Total Count	%	Oblique Total Count	%	Vertical Total Count	%	Total
Tree Bark	14	100%	0	0%	0	0%	14
Flowers	0	0%	18	100%	0	0%	18
Mature Leaves	181	40.3%	241	53.7%	27	6.0%	449
Young Leaves	50	44.6%	48	42.9%	14	12.5%	112
Total	245		307		41		

Use of different tree quadrants while feeding by indri group 55

Indri mainly used quadrant 4 for overall feeding behaviors (Table 6.202). All of the food types eaten by indri were consumed in this quadrant. Leaves were consumed in all quadrants whereas tree bark was only eaten in quadrant 4. For feeding behaviors, indri group 55 maintained the more traditional quadrants in that only the canopy and trunk were used and not other environmental features such as tree falls, liana tangles, etc.

Table 6.202 Quadrant used for food consumption by indri group 55

Quadrant	Quad 1	Quad 2	Quad 3	Quad 4	Quad 5	Quad 6	Quad 7
Tree Bark	0	0	0	14	0	0	0
Flowers	0	4	0	2	0	12	0
Mature Leaves	88	105	42	103	19	66	26
Young Leaves	8	0	6	27	22	14	12
Total	96	109	48	146	41	92	38

Foods consume in different levels of canopy/vegetation connectivity by indri group 55

Indri group 55 frequently engaged in feeding behaviors in forested areas with connected (29.0%) and small-gapped (27.7%) canopy/vegetation but also occupied areas with medium gaps (22.9%). All of the indri young leaf consumption occurred in areas with connected or small-gapped canopy/vegetation, while mature leaf consumption occurred within all of the categories (Table

6.203). Tree bark was only eaten in areas of connected/small gaps while flower consumption only occurred in connected canopy/vegetation areas.

Table 6.203 Different canopy/vegetation distances and foods consumed by indri group 55

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Tree Bark	0	14	0	0	0
Flowers	7	0	11	0	0
Mature Leaves	118	0	153	42	136
Young Leaves	47	65	0	0	0
Total	172	79	164	42	136

LOCOMOTION BY INDRI GROUP 55

Locomotor modes used by indri group 55

Overall indri group 55 spent more time resting and much less time moving out of their entire activity budget. Indri used a variety of different locomotor modes for movement, but the focus was on one to three meter leaps, which collectivity made up 81.6% of their total time spent moving (Table 6.204).

Table 6.204 Locomotor modes used by indri group 55

Locomotor Modes (N=87)	Total Count	Percentage
Climb	3	3.4%
L<1	2	2.3%
L1	20	23.0%
L2	29	33.3%
L3	22	25.3%
L4	9	10.3%
Vertical Bound	2	2.3%
TOTAL	87	100%

Size of substrate used for locomotion by indri group 55

Size of substrate affects movement (K-S, D_{MAX}=0.17, p<0.05). Indri used medium substrates 62.1% of the time with much less focus on small or large substrates (Table 6.205). Medium substrates were used for leaps of one to three meters with variable amounts of time also devoted to small and large substrates for each distance (Table 6.206).

Table 6.205 Different sized of substrates used for movement by indri group 55

Size of Substrate	Small	Medium	Large
Move	18	54	15

Table 6.206 Different sized substrates and locomotor modes used by indri group 55

Size of Substrate	Small	Medium	Large
Climb	0	2	1
L<1	0	2	0
L1	5	13	2
L2	9	17	3
L3	2	16	4
L4	2	4	3
Vertical Bound	0	0	2
Total	18	54	15

Height used by indri group 55

Height of substrate affects movement (K-S, D_{MAX}=0.28, p<0.01). Indri group 55 moved at a range of heights although lower heights and very tall heights were used less frequently than mid-range heights (6-10 meters), which collectively consumed 72.4% of the time out of the total heights utilized (Table 6.207). The indri maintained their full range of leaping distances for all heights. The exceptions included the four meter leaps which were focused in taller heights as well as short leaps of less than one meter. The short leaps were from within-substrate movement while the longer distance leaps are from between-substrate movement (Table 6.208, Figure 6.16).

Table 6.207 Different heights used for movement by indri group 55

Height of Substrate	A	B	C	D	E	F	G	H
Move	1	3	5	18	24	21	12	3

Table 6.208 Heights of substrates and locomotor modes used by indri group 55

Height of Substrate	A	B	C	D	E	F	G	H
Climb	0	0	0	1	0	1	1	0
L<1	0	0	0	0	0	1	1	0
L1	0	1	2	5	5	4	1	2
L2	1	0	2	9	8	7	2	0
L3	0	2	1	3	9	2	5	0
L4	0	0	0	0	2	6	1	0
Vertical Bound	0	0	0	0	0	0	1	1
Total	1	3	5	18	24	21	12	3

Substrate orientations used for different locomotor modes by indri group 55

Orientation of substrate influences indri movement (χ^2=60, df=2, p<0.001). Indri used vertical substrates for movement 70% of the time with only one occurrence of movement on a horizontal substrate. The other 30% of their movement time was dedicated to the use of oblique substrates (Table 6.209).

Table 6.209 Substrate orientations and locomotor modes used by indri group 55

Orientation	Horizontal	Oblique	Vertical
Climb	0	0	3
L<1	0	1	1
L1	0	8	12
L2	1	6	22
L3	0	6	16
L4	0	3	6
Vertical Bound	0	2	0
Total	1	26	60

Quadrant use for movement by indri group 55

Indri moving behavior is influenced by tree quadrant (χ^2=280, df=7, p<0.001). Indri in group 55 occupied quadrant 7, 70.1% of the time for moving behaviors with very little focus on any of the other quadrants other than quadrant 6, which was only used 18.4% of the time (Table 6.210).

Table 6.210 Movement in varying quadrants used by indri group 55

Quadrant	1	2	3	4	5	6	7	Liana	Rav Palm5
Move	1	2	2	1	2	16	61	1	1

Canopy/vegetation connectivity and locomotor modes by indri group 55

The level of canopy/vegetation connectivity affects movement patterns (K-S, D_{MAX}=0.36, p<0.01). Indri group 55 frequently moved through connected canopy/vegetation (56.3%) and areas with small gaps (28.7%) with very little focus towards the other connectedness categories (Table 6.211). The canopy/vegetation connectivity did not affect the locomotor modes used to move through the environment (χ^2=0.78, df=2, p>0.05). The indri moved with their full range of jumping distances regardless of the connectivity factor within the environment they were moving (Table 6.212). Eighty-nine percent of the movement by indri group 55 was between-substrate movement that consisted of one to four meter leaps throughout the forest. Within-substrate movement mainly consisted of short leaps, climbing, and some vertical bounding (Figure 6.16).

Table 6.211 Levels of canopy/vegetation connectedness used for movement by indri group 55

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
MOVE	49	3	25	4	6

Table 6.212 Levels of canopy/vegetation connectedness and locomotor modes used by indri group 55

Distance b/n Canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Climb	1	0	1	1	0
L<1	0	0	1	1	0
L1	13	0	5	0	2
L2	19	1	8	1	0
L3	13	0	7	1	1
L4	3	2	3	0	1
Vertical Bound	0	0	0	0	2
Total	49	3	25	4	6

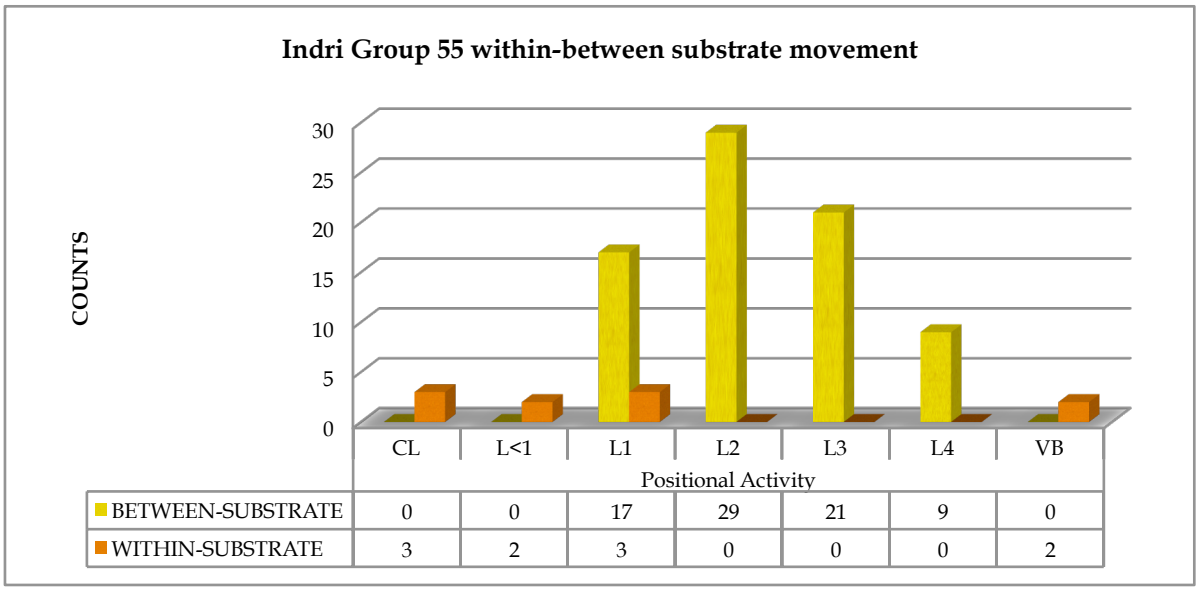


Figure 6.16 Indri group 55 within-and-between substrate movement

RESTING BEHAVIORS BY INDRI GROUP 55

Postures used for resting by indri group 55

The indri spent equal proportions of their time resting in either sit-extend, sit, or vertical cling postures for resting with a very small percentage allocated to recline postures (Table 6.213).

Table 6.213 Postural modes used while resting by indri group 55

Postural Modes for Rest (N=697)	Total Count	Percentage
Recline	12	1.7%
Sit-Extend	248	35.6%
Sit	249	35.7%
Vertical Cling	200	28.7%

Size of substrate used for resting by indri group 55

Indri resting behaviors are influenced by size of substrate (K-S, D_{MAX}=0.17, p<0.01). The indri focused on medium substrates 46.3% of the time as well as large (38.2%) substrates for resting (Table 6.214). Small substrates were also used, but to a much lesser extent (Table 6.214).

Table 6.214 Size of substrate used for resting by indri group 55

Size of Substrate Resting	Total Count	Percentage
Small (1-5 cm)	110	15.5%
Medium (6-10 cm)	328	46.3%
Large (11-15 cm)	271	38.2%
Total	709	100%

Size of substrate used for different resting postural modes by indri group 55

While resting in a recline posture the indri only occupied medium substrates. Resting in a sit-extend posture was also on medium substrates, whereas sitting and resting occurred on large substrates. The indri showed an affinity for medium substrates while vertical-clinging and resting, although the large substrate percentage was relatively high as well (Table 6.215).

Table 6.215 Different sized substrates used for resting postures by indri group 55

Size of Substrate	Small	%	Medium	%	Large	%	Total
Recline	0	0%	12	100%	0	0%	12
Sit Extend	47	19.0%	116	46.8%	85	34.3%	248
Sit	56	22.5%	89	35.7%	104	41.8%	249
Vertical Cling	7	3.5%	111	55.5%	82	41.0%	200
Total	110		328		271		

Substrate orientation used for resting by indri group 55

Indri resting behaviors are influenced by orientation of substrate (χ^2=278, df=2, p<0.001). Indri used oblique substrates 61.6% of the time out of their total resting time (Table 6.216).

Table 6.216 Different orientations used for resting behaviors by indri group 55

Horizontal Count	%	Oblique Count	%	Vertical Count	%	Total
187	26.4%	437	61.6%	85	12.0%	709

Height of substrate and resting behavior by indri group 55

Indri resting behaviors are influenced by substrate height (K-S, D_{MAX}=0.28, p<0.01). The indri used a full range of heights from one meter up to 15 meters for resting behaviors. Rest occurring at the lower heights often was brief rest periods between vertical jumps. The more extensive resting periods occurred in the taller canopy between the heights of 9 and 11 meters (56.8%) (Table 6.217).

Table 6.217 Height of substrate used while resting by indri group 55

Height of Substrate	A	B	C	D	E	F	G	H	I
Rest	2	10	28	73	90	257	146	94	9

Quadrant use and resting behavior by indri group 55

Indri have a preference for certain quadrants while resting (χ^2=700, df=7, p<0.001). The quadrant used for resting showed more variation in the substrates used in comparison to the indri's quadrant use for feeding and moving, which were much more traditional in the sense that the indri only used the canopy and trunk. For rest, the indri also used tree knots, lianas, and ravinala palms (Table 6.218). Despite the increased variety, the indri focused their resting in quadrants 4 (17.6%) and 6 (39.5%).

Table 6.218 Different quadrants used for resting by indri group 55

Quadrant	1	2	3	4	5	6	7	Knot	Liana	Rav Palm4	Rav Palm5
Rest	4	27	70	125	82	280	98	7	2	1	3

Canopy/vegetation connectivity and resting behaviors by indri group 55

The level of canopy/vegetation connectivity affects resting behaviors (K-S, D_{MAX}=0.16, p<0.01). Indri predominantly rested in areas of connected (35.7%), small (28.1%), and medium-gapped (24.8%) areas of the forest (Table 6.219).

Table 6.219 Different levels of connectedness for resting by indri group 55

Distance b/n canopy	Connected	Connected/Small	Small	Small/Medium	Medium
Rest	253	42	199	39	176

INDRI GROUP 55 SUBSTRATE COMBINATIONS AND KEYSTONE STRUCTURES

Substrate Combinations

Orientation of substrate and quadrant use by indri group 55

Indri used a variety of quadrants and orientations for resting behaviors (Table 6.220). Horizontal substrates were principally used in quadrants 1 and 5 while oblique substrates were the

predominate orientation of use in quadrants 2 through 4 and 6. Vertical substrates were used in quadrant 7.

Table 6.220 Orientation and quadrant use by indri group 55

Quadrant	Horizontal	Oblique	Vertical
1	83	29	0
2	67	94	10
3	41	76	3
4	93	179	3
5	116	21	0
6	49	333	18
7	0	57	141
Knot	0	0	7
Liana	2	0	1
RavPalm4	1	0	0
RavPalm5	0	0	4

Height of substrate and quadrant use by indri group 55

Indri used quadrant 7 in the lower heights between 1 and 5 meters (Table 6.221). At the height of six meters, in addition to quadrant 7, the indri also used quadrants 4 and 6. At heights starting at 7 to 8 meters the indri used a more diverse array of quadrants. At the height of 7 to 8 meters the indri focused on quadrants 6 and 7. At the height of 9 to 10 meters the indri used quadrants 4 and 6 while focusing more on quadrant 2 and 5 at the height of 11 meters. At the tallest heights of 12 to 15 meters the indri often used the highest quadrant, 1.

Table 6.221 Height of substrate and quadrant for indri group 55

Height of Substrate	Quad1	Quad2	Quad3	Quad4	Quad5	Quad6	Quad7	Knot	Liana	Rav Palm4	Rav Palm5
A	0	0	0	0	0	0	10	0	0	0	0
B	0	0	0	0	0	7	11	0	0	0	0
C	0	0	0	0	0	19	22	0	0	0	0
D	0	4	0	50	8	45	52	0	0	0	0
E	6	11	5	8	0	78	75	0	0	1	3
F	7	1	35	117	23	190	14	7	1	0	1
G	23	110	38	45	105	30	14	0	2	0	0
H	66	38	42	46	1	31	0	0	0	0	0
I	30	7	0	9	0	0	0	0	0	0	0

Total tree height and height of substrate used by indri group 55

Indri group 55 used a wide range of height of substrate and height of tree combinations. The indri maximized the space available in the tree using lower heights all the way to the tallest heights in the canopy. At the tallest heights of 12 to 15 meters the indri also occupied the tallest substrates (Table 6.222).

Table 6.222 Height of substrate and total height of tree used by indri group 55

	Height of Tree							
Height of Substrate	B	C	D	E	F	G	H	I
A	4			1	5			
B		7			10	1		
C			6	15	12	7	1	
D			3	83	60	11	2	
E				14	127	26	20	
F			1		59	281	54	1
G						141	226	
H							186	38
I								26

Keystone Structures

The indri focused more on moving and feeding trees as important keystone structures and less so on resting trees. A list of these structures is presented in Table 6.223.

Table 6.223 Keystone structures used by indri group 55

Malagasy Tree	Dbh (cm)	Height (m)	Activity	GPS
Famelona	30	11.9	Moving	(0309192, 8018759)
Mampay	42	12.8	Feeding flowers	(0309067, 8018782)
Azinina	30	10.6	Feeding flowers, leaves	(0309093, 8018744)
Lalotina	38	10.3	Moving	(0309250, 8018537)

INDRI 55 NEAREST NEIGHBOR

Identity of nearest neighbor

The radio-collared male in indri group 55 moved, fed, and rested on his own 50% of the time (Table 6.224). When he was with his group, the other group members were the nearest neighbor relatively equal percentages of the time.

Table 6.224 Nearest neighbor for indri group 55

Nearest Neighbor	Focal Male
Female/Juvenile	13
Female	233
Juvenile	206
Pink	249
>20 meters	712

Distance of nearest neighbor

The 50% of the time that the focal male was with his group, he used a wide range of distances to nearest neighbor with the most frequent distances oscillating between one and four meters (Table 6.225).

Table 6.225 Distances of nearest neighbor for indri group 55

Distance (m)	0	1	2	3	4	5	6	8	10	12
Female/Juvenile	8	11	36	57	80	6	10	3	0	12
Female	0	1	0	0	3	0	0	8	1	0
Juvenile	0	31	58	23	60	28	2	3	0	0
Pink male	11	76	70	56	7	27	1	0	1	0
Total	19	119	164	136	147	61	13	6	2	12

Summary Statement Indri Group 55

Microhabitat features influenced group 55's movement, feeding, and resting behaviors. These paragraphs highlight those substrates that indri group 55 utilized at a higher frequency than others, but as noted in the preceding sections, the indri in this group were adept at utilizing a wide range of different heights and substrates for resting, eating, and moving. In summary, indri group 55 used medium substrates at the heights of 9 to 11 meters in quadrants 4 and 6 on oblique

branches. A majority of their time was spent feeding and resting with little time devoted to moving. The total tree height mainly used by indri group 55 ranged from 11 to 13 meters. During each all day follow the substrates that this group used were flagged and identified when possible. The list of the trees used for resting, moving, and feeding is included in the appendix. Indri group 55 used a variety of tree species but showed a heightened preference for some keystone trees for feeding and moving, and to a lesser degree, resting behaviors. Some days the group only foraged from two or three trees. For feeding behaviors group 55 focused on rara leaves (N=10), tavolo fotsy leaves (N=8), and antafonona leaves (N=6). Overall, the most common trees group 55 used for all behaviors included rara (N=21), mampay (N=8), tavolo fotsy (N=14), voapaka keliravina (N=6), and antafonona (N=6).

Indri group 55 spent more than 75% of their time feeding on mature leaves. Similar to indri group 45, indri group 55 also incorporated tree bark into their diet, although to a lesser extent. Feeding by indri was in a sit posture over 50% of the time on medium oblique substrates at the heights of 11 to 13 meters in quadrant 4. The indri foraged in areas with connected, small-gaps, and medium-gaps in the canopy/vegetation.

Indri mainly used one to three meter leaps for movement onto medium vertical substrates between the heights of 6 to 10 meters in quadrant 7 through areas with connected canopy/vegetation.

Indri group 55 rested by sit or sit-extend postures on medium and large oblique substrates at a height of 9 to 11 meters in quadrant 6. The indri used areas of connected, small-gapped, and medium-gapped forest for resting behaviors.

Indri group 55 used a variety of different quadrant and orientation of substrate combinations with no central focus. Oblique and horizontal oriented substrates were used in the peripheral space of the tree as well as space closer to the trunk and core of the tree. The indri group also used multiple quadrants at different heights with the only central pattern being that the

indri tended to use quadrant 7 at lower heights. Additionally, the indri exploited numerous height of substrate and height of tree combinations. Group 55 maximized the space available in a tree, using lower heights all the way to the tallest heights in the canopy.

Indri group 55 consisted of four members. The focal male in the group traveled, foraged, and rested on his own 50% of the time. When he was in close proximity to his group the other group members were his nearest neighbors relatively equal percentages of the time with the most frequent distances ranging from one to four members.

Indri group 55 was flexible in their ability to utilize a wide spectrum of different substrates, orientations, and heights for resting, feeding, and moving behaviors. The have heightened preferences for certain substrates but are also quick to make adjustments and use other forest elements.

The next section will highlight some of the interesting findings observed among the radio-collared lemurs by discussing a comparison between the different groups. Based on similarities the lemur taxa share in terms of structure and moving behaviors, a recommendation for a corridor/connectivity project is subsequently proposed.

SUMMARY OF ALL RADIO-COLLARED LEMUR GROUPS
A COMPARISON BETWEEN LEMUR GROUPS AND MICROHABITAT USE

The following is a comparison between the different radio-collared groups in terms of vegetation structure and behavior with an aim to provide detailed information for a corridor and/or within forest connectivity project, facilitating movement for a lemur community in BNR.

SIFAKA GROUPS 1 AND 10

A comparison of sifaka groups reveals both interesting similarities and differences. The range of sifaka group 1 is located in the northern portion of the forest, whereas the range of sifaka group 10 is located farther south within the research area. Both groups spent comparable

percentages of time dedicated to eating, moving, and resting overall. However, the resting periods for sifaka group 10 were much shorter as this group rarely rested for extended periods of time. The longest resting daily bout averaged a half an hour. Most of the rest behaviors were from the brief periods in between the vertical leaps while the sifaka were deciding the next substrate to jump onto or direction to proceed. Sifaka group 10 was the fastest and most active lemur group followed in this research.

Sifaka group 1's diet included the most variety of food types of all the lemur groups. The sifaka spent the most time feeding on leaves and flowers using a variety of different postures. Compared to sifaka group 1, group 10 maintained a less eclectic diet but with the same general focus on leaves and flowers. Sifaka group 10 incorporated twice as much fruit in their diet compared to group 1 (χ^2=10.13, df=1, p<0.002).

For feeding behaviors sifaka group 1 used small oblique and horizontal substrates at a height of 9 to 11 meters in quadrants 2 and 4. Sifaka group 10 used small and medium oblique substrates at the same height of 9 to 11 meters in quadrants 6 and 7. Both sifaka groups used a broad range of different quadrant types, including all of the quadrants of the tree, but also made use of ravinala palms, epiphytes, and lianas. Sifaka group 10 spent more time in vertical cling postures while feeding in comparison to group 1 (χ^2=62.11, df=1, p<0.0001), which used sit-extend and sit postures a higher percentage of time. Often the sifaka in group 10 were still chewing and holding more of the food item from the previous tree as they moved to the next. The use of vertical-cling postures by sifaka group 10 reflects their drive to be "on the go." Sifaka in group 1 sat in the tree, consumed the food, and then proceeded to the next. Both groups mainly engaged in feeding behaviors in areas of connected vegetation or canopy.

Both sifaka groups primarily moved using 1 and 2 meter leaps. Sifaka group 10 also used <1 meter leaps while sifaka group 1 did not. This perhaps is a reflection of the cluttered dense forest that sifaka group 10 frequently traveled through. The size, height, and orientation, in

addition to the quadrant and level of canopy connectivity, all affected the movement patterns of sifaka groups 1 and 10. Sifaka group 1 used medium vertical substrates at a height of 4 to 10 meters in quadrant 7 in connected canopy/vegetation. Sifaka group 10 focused almost equal amounts of effort on small and medium-sized vertical substrates for movement while sifaka group 1 used medium sized substrates a slightly higher percentage of the time. Sifaka group 10, in contrast to group 1, moved at a very low height of one meter a majority of the time, and even used the ground (χ^2=41.09, df=1, p<0.0001). Although the focus was on quadrant 7, sifaka group 10 made use of a variety of different types of substrates to move, including fallen trees, lianas, and ravinala palms. The level of connectivity did not affect their locomotor position. The sifaka still maintained their full locomotor repertoire regardless of the level of connectivity.

The size of substrate, orientation, height, quadrant, and degree of connectivity all influenced sifaka resting behaviors. Both sifaka groups occupied small and medium oblique substrates at a height of 9 to 11 meters in quadrant 6 in areas of connected canopy/vegetation. The sifaka in group 10 used a more eclectic set of quadrants for their resting behaviors, including dead trees, ravinala palms, lianas, and liana clusters. This broad scope of use echoes the short stints of rest observed during movement, a behavior that also utilized a diverse array of quadrants.

Both sifaka groups used different substrate orientations in different quadrants. For example, the sifaka used horizontal substrates in quadrant 5 and oblique in quadrant 6. This may be an active choice by the lemurs or use driven by the natural tree growth such that more horizontal branches are available in the periphery of the tree and oblique branches are available closer to the trunk. The sifaka used a broad range of different height and quadrant combinations. Their affinity for quadrant 6 was often utilized at the corresponding height of 7 to 10 meters. As mentioned previously, the sifaka in group 10 occupied a wider range of quadrants for movement. The total height of the tree did not appear to impact the sifaka's use of the tree. Often the height of the substrate used by the sifaka was also the total height of the tree. This is especially true for

shorter trees with narrow crown volume where the sifaka monopolized the entire crown space with their body.

Sifaka group 1 integrated important keystone structures into their home range. These keystone structures primarily focused on feeding behaviors and to a lesser extent moving and resting. While the sifaka routinely returned to the same feeding trees, substrates used for resting and moving were more variable. Sifaka group 10 also included keystone structures in their daily routine. Similar to group 1, sifaka group 10 occupied particular feeding trees, but group 10 also had specific moving trees and substrates. Both groups lacked preferred resting trees.

Variation in social spacing was observed between these two sifaka groups. In sifaka group 1, the focal female spent a majority of her time alone. When she was with her other group members she spent equal amounts of time either in contact or less than one meter away from both the male and the other female. Sifaka group 10 was much more cohesive and moved, fed, and rested together as a unit. In group 10, the radio-collared male was on his own only 3% of time in contrast to group 1, where the female was on her own 73% of the time. The autonomy of the sifaka female in group 1 may reflect her pregnancy and then birth of her infant. Although, the other female in group 1 also gave birth but appeared to be in closer contact to the male. The full extent of the other female and male's social proximity is unknown due to the focus on following the radio-collared female. The health assessments conducted on the lemurs during the initial darting indicated they were healthy and free of external parasites. Plus, the pregnancies of the two females in group 1 suggest that these groups are obtaining proper nutrition in the designated ranges they reside, suggesting that their social spacing may not be the result of patch quality but of some other complex social component of primate group life.

In sum, both sifaka groups were quite flexible in their ability to use a wide range of different substrates, orientations, and heights for resting, feeding, and moving behaviors although both groups demonstrated a preference for certain vegetative attributes over others. The sifaka

expressed a higher frequency of use of certain substrates but were quick to use others when their preferred vegetative attribute was unavailable. Prolific eurytopic species are argued to fare better when faced with environmental challenges such as anthropogenic habitat degradation. The sifaka residing in BNR are by no means "weedy," and yet the population seems stable and may be increasing evidenced by the birth of infant sifaka during this research. Why the population remains so small is of much interest and is addressed further in the discussion chapter.

A COMPARISON OF BOTH SIFAKA GROUPS AND EULEMUR GROUP 34

Only one brown lemur group was followed in this research. The group followed consisted of one female and two juveniles, one juvenile younger than the other. This was an interesting group composition as most of the brown lemur groups in BNR consist of several adult males and females. Similar to sifaka group 10, the range of the brown lemurs was in the southern portion of the research area. Brown lemurs, in general, are ecologically flexible in that they have been observed to use a broad range of habitat types (including anthropogenically altered habitat) and incorporate a range of food items into their diet both on a daily basis and seasonally. Results from this research indicate that sifaka groups 1 and 10 are ecologically flexible and fare well in the heterogeneous landscape of BNR. This makes for an interesting comparison with the brown lemur group followed in this research.

Variation in activity budget and structures used for different behaviors between the sifaka and brown lemurs was observed. Compared to both sifaka groups, the brown lemurs spent a greater percentage of their time resting (χ^2=81.94, df=1, p<0.0001). Differences in feeding behavior were also observed. The brown lemurs incorporated a higher percentage of both fruits and flowers in their diet with less emphasis on leaves. The brown lemurs were also observed to lick nectar from flowers, a behavior not observed among the sifaka. The brown lemurs frequently stood or sat while feeding on all of the different food types incorporated into their diet. The brown lemurs used

very small and small substrates and rarely medium or large substrates while feeding. This contrasts with the sifaka groups that incorporated higher percentages of medium substrates for feeding with much less focus on very small (χ^2=20.1, df=1, p<0.001). These three groups share a lack of focus on large substrates for feeding. Similar to the sifaka groups, feeding typically took place at a height of 9 to 10 meters. Oblique substrates were the main orientation used for feeding in quadrants 3 and 5. While the sifaka focused their feeding behaviors closer to the trunk of the tree, the brown lemurs had an affinity for more peripheral space. In addition, the sifaka used external quadrants, like lianas and ravinala palms, more frequently than the brown lemur group. The brown lemurs foraged for food in areas of connected canopy/vegetation and small gaps similar to the sifaka groups.

The brown lemurs moved by quadrupedal locomotion with the occasional small leap onto both small substrates and very small substrates at a height of 7 to 8 meters. Quadrupedal locomotion occurred at all heights with more leaping at heights above six meters. Both sifaka groups and the brown lemurs demonstrated variation in the heights used for movement. The brown lemurs used oblique and horizontal substrates and to a lesser extent vertical substrates. In contrast, both sifaka groups used vertical substrates to a greater extent for moving behaviors. The shared orientation for all three groups was oblique substrates. The brown lemurs made use of quadrant 5 and lianas for movement. The sifaka mainly used quadrant 7, although sifaka group 10 also incorporated many external environmental features for movement as well. Akin to the sifaka, the brown lemurs moved through connected canopy/vegetation. In contrast to the sifaka, canopy connectedness also affected the mode of locomotion used by the brown lemurs. The brown lemurs moved by quadrupedal locomotion in all of the quadrants but leapt more in areas of connected canopy/vegetation.

Unlike the sifaka, the brown lemurs rested for extensive periods of time huddled together with their tails wrapped tightly around one another. Most of the brown lemur resting occurred on

small and medium oblique substrates between the heights of 7 and 11 meters, attributes comparable to the sifaka resting behaviors. The brown lemurs maintained a broad range of quadrant use for resting, focusing on quadrants 3, 4, 5, 6 and the use of lianas, ravinala seed pods, and liana tangles. Both sifaka groups focused their resting more so in quadrant 6 with sifaka group 10 expressing more variation. Resting behavior was a large percentage of the brown lemurs' activity budget, perhaps permitting them to expand out to a broad range of sleeping quadrants. All three groups of lemurs rested in areas of connected canopy/vegetation.

Distinct from the sifaka groups, the brown lemurs used oblique substrates more frequently in all quadrants of the tree. The brown lemurs predominantly used lianas and liana tangles below the height of seven meters. Other than this distinction, no pattern emerged of a quadrant preference at a particular height. This pattern was also true for the sifaka groups. Similar to the sifaka groups, the total height of the tree did not influence the height of substrate used for the brown lemurs.

Keystone structures were documented for the brown lemurs. Unlike the sifaka groups, key resting trees were important to the brown lemurs. One particular ravinala palm was used frequently by the brown lemurs for daily rest in addition to overnight rest. The brown lemurs also routinely used the same moving and feeding trees. Many of the areas the brown lemurs utilized were ensconced in thick vine growth and liana tangles, also making these important keystone structures that may dictate the space used by the brown lemurs. The brown lemurs often used these cluttered areas as points of refuge for resting as well as feeding. When these features were available in their path of travel, the brown lemurs purposely moved right through them.

Compared to both sifaka groups, the brown lemurs had the highest percentage of constant group cohesion. No group member was ever more than four meters away from the other group members. This was the case for foraging, resting, and moving behaviors.

Much of the variation in microhabitat structure use existed within the brown lemur's resting behaviors. Furthermore, they did not demonstrate much variation in the food types or different plant species consumed, focusing on a few key fruit trees. Brown lemur group 34 was often chased out of feeding trees by other larger brown lemur groups or even by other larger-bodied lemur species. Single ruffed lemurs were observed to chase the brown lemur group out of fruit trees on several occasions. The brown lemur group waited in an adjacent liana tangle or tree covered in vines until these other lemurs were finished feeding in the fruit tree and moved on and only then did the brown lemur group recommence their own foraging behavior.

A COMPARISON OF INDRI GROUPS 40 AND 45

Indri group 40 consisted of a solitary female, Lenore. Lenore spent almost equal amounts of time eating and resting. She often sat in the same tree for hours consuming large quantities of mature or young leaves. She sat on medium horizontal or oblique substrates in quadrant 4 between the heights of 6 and 13 meters in areas of connected canopy/vegetation. Indri group 45 consisted of one male (Howard) and one female (Sue). Indri group 45 also spent almost equal amounts of time resting and eating. Lenore consumed a significant percentage of young leaves in comparison to group 45 (χ^2=11.24, df=1, p<0.001) while group 45 consumed a higher percentage of flowers (χ^2=6.53, df=1, p<0.01). Group 45 was the only group that incorporated a significant percentage of bark into their diet in comparison to the other indri groups. Britt et al. (2002) also observed the consumption of bark by indri groups in BNR. They documented that immature leaves were the preferred food item, but during times of resource scarcity, the indri consumed bark along with mature leaves, fruits, and seeds as substitute food items.

Lenore consumed the highest percentage of young leaves in comparison to all five indri groups (χ^2=16.91, df=1, p<0.0001). Lenore used fairly equal percentages of small and medium substrates for feeding; indri group 45 focused more so on medium substrates. Both groups foraged

at the heights 9 and 13 meters but Lenore also used lower heights to forage. Both groups used horizontal and oblique substrates for feeding behaviors although Lenore used a slightly higher percentage of horizontal substrates but this is not significant (χ^2=1.75, df=1, p>0.09). Both groups used quadrant 4 for most of their feeding behaviors. Lenore was more apt than group 45 to use other quadrants beyond the tree canopy and trunk. She also incorporated lianas and tree knots as viable substrates for feeding postures. Both groups mainly foraged in areas of connected canopy/vegetation. Lenore also spent much of her foraging time in areas that were connected with some small gaps while group 45 foraged in more open, less-connected areas composed of small and medium gaps.

The size and height of the substrate did not affect Lenore's movement. She used small, medium, and large substrates an equal proportion of the time between the heights of 4 and 10 meters. Similar to Lenore, the size of substrate did not affect movement for group 45, but the height of substrate, in contrast, did affect movement for group 45. Group 45 used lower heights for movement but most of their focus was at heights above 7 meters. The orientation and quadrant affected the movement patterns of both indri groups with all indri focusing on vertical substrates in quadrant 7. The level of canopy connectedness affected her movement as well as the locomotor mode she used to negotiate different degrees of connectivity. Lenore mainly moved through areas of the forest consisting of connected canopy/vegetation, using one meter leaps more frequently. When she moved through non-connected areas, she focused more so on three and four meter leaps. The movement of group 45 was affected by the degree of connectivity. Group 45 focused their movements through areas of connected canopy/vegetation. Unlike Lenore, the locomotor mode was not affected by connectivity, where this group used their full range of locomotor modes regardless of the connectedness of the forest. For example, in areas with connected canopy the indri moved by one meter leaps and in areas of medium gaps the indri still moved by one meter leaps.

The size of substrate, orientation, height, quadrant, and degree of connectivity all affected Lenore's and group 45's resting behavior. Lenore mainly rested on medium and large oblique substrates in a sit-extend posture at a height of 10 meters in quadrant 6. Lenore rested in areas of connected canopy/vegetation. Group 45 also rested on medium and large oblique substrates between the heights of 7 and 11 meters in quadrant 6. Similar to Lenore, group 45 also rested in areas with connected canopy/vegetation but also frequented areas with small gaps in their environment.

Lenore used horizontal substrates within the peripheral quadrants of the tree and oblique substrates in quadrants closer to the trunk of the tree. Group 45 demonstrated more diversity in the orientation and quadrant used. For example, group 45 used horizontal substrates in central and peripheral quadrants of the canopy and also varied their use of different orientations even within the same quadrant. Lenore and group 45 both used different quadrant and tree height combinations. For Lenore, the most frequent use was quadrants 4 and 6 at the height of 9 to 10 meters and quadrant 5 was used more frequently in taller heights of the canopy. Indri group 45 spent the most time in quadrant 6 regardless of the height although at taller heights in the canopy the indri spent more time in peripheral positions. Lenore and group 45 used a full range of different height of substrate and total height of tree combinations. When taller trees were occupied the indri also used taller substrates, maximizing their use of the entire tree crown.

The range that Lenore used encompassed a wide variety of different habitat types, including areas of low canopy and dense understory to more open areas with 15 meter canopy. Lenore used keystone structures in her range on a regular basis for feeding, moving, and resting. Often these same keystone structures were used for all three behaviors. For example, one day she may use an azinina tree for feeding and the next for moving. Or, she may rest in the azinina tree in the morning and then return to the same tree later on in the day for feeding. Lenore frequently used tree knots for feeding postures. She also repeatedly used the same tree knots in her keystone feeding trees

perhaps indicating these tree attributes also as important structures for Lenore that she actively seeks out as an important component of her feeding ecology. Group 45 included important keystone trees into their daily activity budget for resting, moving, and eating. Similar to Lenore, group 45 also used the same keystone tree for multiple purposes.

Akin to Lenore, the female, Sue, from group 45 spent more than 50% of her time by herself more than 20 meters away from the male in her group. Group 45 had the least group cohesion of all the indri groups.

A COMPARISON OF INDRI GROUPS 50, 55, AND 14

Variation in activity pattern and moving, resting, and feeding behaviors were observed among indri groups 50, 55, and 14. Similar to groups 40 and 45, indri group 55 spent relatively equal proportions of time resting and eating with the least amount of time devoted to moving. Group 50 spent the greatest percentage of time resting in comparison to eating (χ^2=141.36, df=1, p<0.0001) while group 14 spent the most time eating in relation to resting (χ^2=6.52, df=1, p<0.01). Group 55 was the only other group, besides group 45, observed to consume bark. The percentage of bark in the total diet of indri group 55 was much less than for group 45 (χ^2=31.27, df=1, p<0.0001). Group 14 was the only indri group observed to eat seeds. All three of these indri groups used medium substrates more than 50% of the time for resting behaviors with more emphasis of use towards small substrates in comparison to large substrates. Indri groups 55 and 50 mainly fed at a height between 9 and 11 meters, whereas group 14 fed at the heights of 9 to 10 meters and 12 to 13 meters, skipping over the 11 meter height. Group 55 also spent a higher a percentage of their time occupying substrates between the heights of 12 and 13 meters for feeding behaviors. Group 50 used this taller canopy height, albeit at a much lower percentage in relation to the other primary heights for feeding. All three groups spent the most time on horizontal and oblique substrates. Group 14 focused a higher percentage of time towards horizontal substrates while groups 50 and 55 utilized oblique substrates more often for feeding postures (χ^2=15.62, df=1,

$p<0.0001$). Indri groups 14 and 55 occupied quadrant 4 more often for feeding, while indri group 50 primarily used quadrant 1. Indri group 50 was the only indri group out of these three to use substrates other than the tree canopy or trunk while foraging. For example, indri group 50 also made use of lianas and liana tangles. As mentioned in the preceding section, Lenore also used lianas and tree knots as substrate quadrants while feeding. Indri group 45 was observed to make use of a liana only once during feeding behaviors. Indri group 14 frequented areas with small gaps in the canopy/vegetation for feeding, whereas indri groups 50 and 55 predominately fed in areas with connected canopy/vegetation. Indri group 14 also made equivalent use of areas with connection or medium gaps. Indri group 55 made secondary use of areas with small gaps while indri group 50 made secondary use of areas with medium gaps. All three groups demonstrate flexibility in their use of a wide range of different connectivity levels.

Indri groups 14, 50, and 55 were all affected by the size of substrate for movement with all three groups using medium substrates more frequently than other sizes. The indri moved through their environment using one, two, and three meter leaps, although indri group 50 utilized three meter leaps less frequently than the other two groups. The height of substrate, orientation and quadrant collectively affected the indris' movement patterns. Groups 50 and 55 moved in the height range of 6 to 10 meters while group 14 moved within a slightly higher range of 7 to 11 meters. The indri used vertical substrates in quadrant 7 for movement. All five indri groups demonstrated more variability in their use of a wider range of quadrants for movement than for feeding behaviors, including the use of lianas, ravinala palms, and even fallen branches.

The level of canopy connectedness affected all three groups, with the indri predominately moving through connected areas except for indri group 14, which also incorporated a high percentage of time to areas consisting of small/medium gaps. The level of connectivity did not affect the locomotor mode used by indri groups 50 and 55. The indri used their full range of jumping distances regardless of the degree of connectivity. In contrast, the degree of connectivity

did affect the locomotor mode for indri group 14. In areas of connected canopy/vegetation the indri mainly moved by one meter leaps and by two and three meter leaps in areas of small or medium gaps.

Size of substrate affected resting behaviors for indri groups 14, 50, and 55. Indri groups 14 and 50 used medium substrates more than 70% of the time. Indri group 55 used medium substrates approximately 50% of the time in addition to their frequent use of large substrates for resting behaviors.

The orientation, quadrant, and height of substrate, as well as the level of connectivity, affected resting behavior. Indri group 55 used oblique substrates at a height of 9 to 10 meters in quadrants 4 and 6. Indri group 50 used horizontal substrates between the heights of 6 and 10 meters in quadrant 6. Indri group 14 spent equal amounts of time on horizontal and oblique substrates within the heights of 9 to 10 meters also in quadrant 6. All three groups demonstrated more variation in their use of quadrants while resting, especially group 55 that made use of tree knots, lianas, and ravinala palms. Indri in groups 55 and 50 primarily rested in areas consisting of connected canopy/vegetation, whereas group 14 focused more of their time in areas with small gaps.

All three indri groups used a variety of different quadrant and orientation of substrate combinations with no central preference. Oblique and horizontal oriented substrates were used in the peripheral space of the tree as well as space closer to the trunk and core of the tree. The indri groups also used multiple quadrants at different heights with the only central pattern being that the indri tended to use quadrant 7 at lower heights. Additionally, the indri groups exploited numerous height of substrate and height of tree combinations. Groups 50 and 55 often maximized the space available in a tree, using lower heights all the way to the tallest heights in the canopy. Group 14 leaned more towards the taller heights of the tree regardless of the crown volume and shape.

All three indri groups incorporated important keystone structures into their activity budget for resting, feeding, and moving. While indri group 55 focused more on repetitive use of certain moving and feeding trees, indri groups 50 and 14 also incorporated important resting structures into their list of keystone structures. This focus on resting trees is especially the case for group 50 where resting made up the largest percentage of their activity budget.

Indri group 55 consisted of four members. The focal male in this group rested, foraged, and traveled on his own 50% of the time. When he was in close proximity to his group, the other group members were the nearest neighbors relatively equal percentages of the time. The most frequent distances to a nearest neighbor ranged from one to four meters. Indri group 50 consisted of five members. The focal male spent 24% of his time more than 20 meters away from the other group members. When he was traveling, feeding, and resting with the other group members, he was often in close proximity to the juvenile or the adult female with the blue collar. Both the juvenile and the adult female varied in distance to the focal male, ranging from close contact all the way to 15 meters. Indri group 14 consisted of three members. The focal female in this group spent 30% of her time on her own more than 20 meters away from the nearest group member. When she was with her group the most frequent nearest neighbor was the juvenile. The distance between them was variable, ranging from close contact up to 15 meters. In sum, all five indri groups were quite flexible in their ability to use a wide range of different substrates, orientations, and heights for resting, feeding, and moving behaviors. The indri groups, similar to the sifaka, do have preferences for certain substrates.

Microhabitat Summary

One of the goals of this chapter was to determine the importance of small-scale attributes (microhabitat) and keystone structures in lemur patch choice. All eight lemur groups were affected by microhabitat features within their resting and moving behaviors. The lemurs expressed a

heightened preference for some features, which may be driving their patch choice. However, the lemurs were not so connected to these micro-attributes that they became debilitated in their absence. It is also interesting that there are intra-group differences. The comparison of the sifaka groups reveals that the sifaka are flexible in their ability to utilize a range of different substrates. For example, the sifaka in group 10 move at much lower heights in the forest and take advantage of many different types of substrates that fostered their mobile lifestyle. As part of this mobile lifestyle, the sifaka used important keystone structures for movement, whereas sifaka group 1 focused more so on important feeding trees. The indri groups also demonstrated variation in their substrate use and use of keystone structures, suggesting that indri are flexible in adjusting their behavior to the microhabitat available to them in the environment. For example, the range of indri group 14 was highly variable in terms of canopy height, large patches of longoza, and significant gaps in the forest due to tree falls and the natural topography of the landscape. Indri group 14 thus used many areas with small or medium gaps, which consequently affected their locomotion. The indri made frequent use of shorter leaps in the connected vegetation, whereas they expanded these leaps to three or four meters in areas with larger gaps. The other indri groups primarily focused their activities in areas with connected canopy/vegetation, with the different levels of connectivity not affecting their locomotor repertoire.

The flexibility observed by the eight focal lemur groups allowed them to collectively continue to exist in this small forest fragment, benefiting from the heterogeneous landscape. Thus, within patch heterogeneity has a positive affect on the focal lemur groups with the exception being the one group of brown lemurs (Group 34), which may be an anomaly. Despite the limited space in BNR, the fact that it is heterogeneous space compensates for this and allows for a total of eleven lemur taxa to co-exist.

CORRIDOR DESIGN

A component of this research was to identify particular forest attributes for single species, but also for primate communities, with one of the applicable goals to provide useful information for an effective corridor project. Corridors are regions of the landscape that facilitate movement among indiviudals, genes, and ecological processes (Chetkiewicz et al., 2006). Integrating pattern and process is important to emulate functional connectivity throughout the landscape (Chetkiewicz et al., 2006). Animals are unlikely to move within a corridor if they perceive the environment as unsuitable. Habitat selection is a behavioral process that organisms use to actively choose resources (Johnson, 1980) that presumably maximizes fitness (Garshelis, 2000). An organism may select suitable habitat in a variety of ways (Clobert et al., 2001). Quantifiying the details of habitat selection and movement processes might be important for corridor design (Chetkiewicz et al., 2006). However, it is difficult to prescribe a general model for a corridor that would be applicable to multiple organisms (e.g. Beier and Loe, 1992).

In BNR, because of the lemurs' flexibility and ability to use many types of substrates, it is difficult to recommend or "build" the perfect substrate to enhance functional connectivity for a corridor project. If locomotor patterns are focused on with the primary objective to facilitate movement, this research suggests building oblique small (1 to 5 cm dbh) and medium (6 to 10 cm dbh) structures 7 to 8 meters in height within one to two meters of each other. Those substrates located at a distance of two meters from the next should also be fitted with small or very small (<1 cm dbh) oblique or horizontal substrates in a simulated quadrant 5 that connects with the adjacent oblique substrate. All eight lemur groups demonstrated a wide range of use of different substrate types (e.g. ravinala palms, lianas, vines, etc.), indicating that the material used to build the substrates to encourage movement could be variable. The difficult component of this project is duplicating connected canopy/vegetation in the pathway of movement, especially if a corridor is to be built in a fairly open area. The lemurs in this research predominately moved through areas with

connectivity, except for group 14 that moved frequently through open areas as well. Perhaps the trees chosen for replanting in the corridor pathway could be planted at least as one to two meter treelets and not as seedlings in order to simulate more connectivity or coverage. This, in addition to fast growing bushes, lianas, or shrubs could be another avenue to facilitate the use of the corridor. Only three of the five diurnal species were part of all-day follows and provided information for the above recommendation. However, based on behavioral data collected from the point counts, it appears that this recommendation also would benefit bamboo lemurs, but not ruffed lemurs. Ruffed lemurs are the limiting factor. Ruffed lemurs were only observed in one patch of primary rainforest as part of the point counts and opportunistic sightings were also rare. When they were observed in the forest, they moved in the tallest trees 16 meters and greater through connected canopy, requirements that would be difficult to recreate.

Human-made bridges are being used in Madagascar, as discussed in chapter 1, to increase habitat connectivity. The suspension and plank bridges built as part of the Ambatovy Nickel Mining Project accommodate movement for six of the thirteen lemur taxa that inhabit the surrounding forests, although the lemurs utilize the ground to cross the gaps as well (Mass et al., 2011). The bridges do not appear to be based on lemur habitat use or locomotion patterns, but the six lemur taxa (*Avahi laniger*, *Cheirogaleus major*, *Eulemur fulvus*, *E. rubriventer*, *Hapalemur griseus*, and *Propithecus diadema*) still use them, which is quite remarkable and speaks to the behavioral flexibility of lemurs. Bridges that are based on behavioral data may increase the frequency of use by the targeted species. Corridor projects require detailed information of the taxa of interest. Identifying important source habitats in addition to learning about the process of habitat selection and movement patterns are needed to manage habitat in a way that promotes functional connectivity (Chetkiewicz et al., 2006). A practical application of this research is the capacity to build functional bridges and corridors based on keystone and common structures used by a community of lemurs. The habitat requirements of charismatic animals (Simberloff, 1998), like

lemurs, might be able to encompass the needs of other organsims (e.g.umbrella effect) in the environment.

This section demonstrated that microhabitat affects, although to varying degrees, lemur resting and movement patterns in BNR. The next section of this chapter addresses the macrohabitat as an additional important component in lemur patch use. The results, as discussed below, indicate that the macrohabitat *per se* does not affect movement and habitat use among the lemur taxa followed in BNR. A series of plots were quantified in each of the ranges utilized by the different lemur groups following the same methodology used for quantifying the eight patches. The results are presented below highlighting the different plots representative of the different sections of the ranges frequented by the eight radio-collared lemur groups. The results are also represented in a GIS landscape model (Figure 6.18).

Section II: MACROHABITAT

This component of this chapter provides a comparison between the radio-collared lemur groups in the context of the importance of heterogeneity and how patch configuration and composition affect lemur movement patterns and patch use in BNR. The additional plots quantified in the home ranges of each of the lemurs are discussed. These plots, along with their associated attribute data, were analyzed in a GIS and presented as a visual map at the end of this chapter.

Eulemur 34

The quantified plots that *Eulemur* mainly utilized were structurally homogenous with some variation in plant composition. The average height of the first canopy layer in all the plots was 4 m, the second layer 6 m, and the third 9 to 11 m. The plots contained no emergent trees. The density of 6 to 10 cm dbh trees averaged around 11/100 m^2 while 11 to 20 cm dbh and 21+ cm dbh averaged at four and three trees per 100 m^2. The canopies were primarily connected, with the occasional small or medium gap. All plots contained longoza of varying amounts from 25 to 100 m^2

pockets to single stems and viney bamboo that took over the forest floor and the vertical space up to about 6 or 7 meters. The liana density averaged 28/100 m^2 with a range from 12 to 48 per plot. In every plot there was at least one standing dead tree and three dead fallen trees. Although structurally similar, the predominate plants in each plot varied. Plot 1: hasina lavaravina (N=21), mampay (N=17), sadoka beravina (N=17); Plot 2: hazomainty keliravina (N=21), hazontoho (N=17), hazomboany (N=15), Hasina keliravina (N=14), sadoka beravina (N=12); Plot 3: hazomainty keliravina (N=20), hazontoho (N=14), tsimamasatsokina (N=14), famelona (N=13); and Plot 4: hasina lavaravina (N=14); Plot 5: afopotsy (N=6), hazomainty beravina (N=6), tsimamasatsokina (N=6).

The only quantified patch that *Eulemur* group 34 was observed to use was Patch 1600. However, this was not a regular area the brown lemurs returned to during this research. The brown lemurs in group 34 used a small concentrated area (2.6 ha) (Figure 6.17) with few habitat types. The habitat the brown lemurs utilized largely consisted of dense 1 to 5 cm dbh trees, liana tangles, small pockets of longoza, and tree falls that created gaps in the otherwise connected canopy or surrounding vegetation. There was heterogeneity within the plot in terms of different substrate types but all of the plots expressed the same heterogeneity, making the plots used by the brown lemurs fairly similar. The main limit for these brown lemurs might be social boundaries (as discussed in chapter 5) and not necessarily the inability to use different patch types. Brown lemur group 34 provided an important example of how even an ecologically flexible genus may have limitations in their patch use because of space constraints. This group may be locked into this more homogeneous area by the range boundaries of other lemur groups. The small range of the brown lemurs included several fruit trees that they returned to on a regular basis. Perhaps these fruit trees within this smaller area are critical keystone elements that allowed the brown lemurs to use this smaller range with no apparent ill effects.

Indri 14

The range used by Indri 14 did not include many different habitat types. The range used by indri 14 included a succession of steep inclines. The slope of the landscape varied from 31 to 51 degrees. The steep incline of the landscape created a staggered canopy effect in the areas primarily used by the indri. Many of the areas used by indri group 14 contained dense understory with many (58/100 m^2) 1-5 cm dbh trees ≤ 1 meter apart. The plots also contained abundant ravinala palms 9 meters in height, especially on steep slopes. The ravinala palms often had dead palms that monopolized much of the vertical space. Variation existed in the connectivity of canopy layer three. For example, the canopy of plot 8 consisted of small and medium gaps at a height of 11 to 12 meters, while plots 4 and 6 maintained small gaps at a height of 10 meters and connectivity existed at a height of 9 meters in plot 1. Plot 4 consisted of a 225 m^2 area of longoza growing over a small stream also with abundant bamboo and vine tangles extending up to 7 meters in the canopy. The indri frequented this area and negotiated the longoza with no problem by crossing through a narrow area that was only 4 meters wide. The predominate plant composition varied among the plots. Plot 1: mampay (N=7); Plot 2: voapaka madinidravina (N=17); Plot 3: maroando (N=18); Plot 4: lalontina (N=7); Plot 5: hazondomohina (N=7); Plot 6: tavolo fotsy (N=7).

The range of indri 14 did not include any of the quantified patches and the plots for their range were relatively similar with the main difference including the longoza in plot 4. Indri 14 did not demonstrate much variation in the use of different habitat types within their small range (7.2 ha) (Figure 6.17). The smaller range used by the indri is interesting in that the male (7.3 kg) and female (8.4 kg) in this group are the largest-bodied individuals relative to the other lemur groups in this research. This group also spent the highest percentage of time feeding out of their total activity budget. The small range of indri 14 was nested within the ranges of the other indri groups to the east, west, and south. Perhaps the presence of the other indri groups in the surrounding area limited their ability to expand more heterogeneity into their movement and habitat use. No radio-

collared indri group used the space to the north or immediate west, but groups that most likely incorporated this space into their range were heard calling from the west. On one occasion indri group 14 ventured a little further west only to turn back towards the east when another group was heard giving their "honk" vocal alarm.

The area of the forest the indri used was less heterogeneous than other areas and perhaps out of necessity this group was forced into an area that was more homogeneous. Intra-species competition caused a subordinate indri group to decrease their range size, potentially limiting their resource usage. Groups that are suppressed in this way may be more subject to the negative effects of anthropogenic change due to the inability to diversify their range use. The indri in BNR have one of the higher population numbers (~ 100 individuals). The population as a whole may appear to be healthy, but individual groups may be suffering and vying for space. Sifaka, the rarest lemur taxon in BNR (~ 20 individuals), superficially is an unhealthy population size but the individual groups appear to be "benefiting" from their rarity by using large range sizes (compared to indri), allowing the groups to incorporate a large resource base into their habitat use and movement patterns. The low level of intra-species competition experienced by the sifaka in BNR may allow these remaining groups to continue to prosper in this forest fragment.

Indri 40

The range that Indri group 40, or Lenore, used consisted of a variety of different patch types. Plot 1 contains prominent 1 to 5 cm dbh trees and liana tangles that extend up to 6 meters with an 83.4% canopy cover. All three of the canopy layers are connected and the trees are equally spaced. Plot 1 is dominated by moroando trees and contains the only dead tree out of all of the quantified plots. Plot 3 contains anatafonona (10/100 m^2) and abundant pandanus and apanga palms (13/100 m^2) with less emphasis of 6 to 10 cm dbh (6/100 m^2), 11 to 20 cm dbh (2/100 m^2), and 21+ cm dbh (4/100 m^2) trees. The canopy layers in this plot are connected, including a fourth canopy height of 12 meters. The trees and palms are equally distributed. Plot 5 was located in a

small valley with abundant apanga (11/100 m^2) and more prevalent 6 to 10 cm dbh density of 6 to 10 cm dbh trees (10/100 m^2). The trees are spatially clumped with proximity of less than one meter up to 4 meters apart. A fourth 12 meter canopy layer existed here with small gaps. The dominant tree is hazomboangy (13/100 m^2). A small stream runs through this plot. Plot 6 is located in a steep area (slope=40°) consisting of large boulders. Lianas form dense tunnels while tree falls form 10m^2 open areas. The third canopy layer is inconsistent and contains small and medium gaps. The trees, predominately 6 to 10 cm dbh, are clumped ranging from less than one apart up to four meters. Plot 6 is the only plot to contain ravinalas (2/100 m^2). There are also six fallen dead trees. Plot 6 contains a high density of famelona trees (14/100 m^2).

The forest that Lenore used encompassed a wide range of different habitat types, including areas of low canopy and dense understory to more open areas with 15 meter canopy. Lenore's path often seemed an indirect route to the feeding or resting tree and she rarely took the same path twice, traversing different habitat types. All-day follows with Lenore often involved exploring new areas that had not been traveled through during the previous follow. Lenore did not incorporate any of the quantified patches into her range (9.0 ha) (Figure 6.17) although her eastern boundary bordered the western section of Patch Sahabefoza. Lenore maximized her use of different habitat types especially in the southern portion of her range. Other indri groups bordered Lenore's range to the east, providing ample space for Lenore to extend her range farther south and making use of more habitat types. Even though Lenore was a solitary female, she occupied a relatively large range size, especially in comparison to indri groups 50 and 14. This may in part be due to Lenore's ability to expand her range further south while the ranges of indri groups 14 and 50 were nested within the confines of other groups, perhaps limiting their ability to enlarge their ranges.

Indri 45

Indri 45 maintained a heterogeneous range. A 20 m^2 field of longoza is located before plot 1 that runs into the valley and ends adjacent to a small stream. The indri consumed bark in a single

antafonona tree located in the middle of a 25 m^2 pocket of longoza. There are no 21+ cm dbh and this plot is distinguished by having a low count of 6 to 10 cm dbh trees (6/100 m^2). Plot 3 is dominated by mampay trees (25/100 m^2), includes no 11 to 20 cm dbh trees, and consists of a 13 meter fourth canopy layer with medium gaps. Plot 4 also has medium gaps in the fourth canopy layer. Plot 5 maintains a high count of 1 to 5 cm and 6 to 10 cm dbh voapaka madinidravina trees (29/100 m^2). These trees are equally spaced ≤1 meter apart. The 12 meter canopy layer four is connected. Plot 7 has a high count of 21+ cm dbh trees (6/100 m^2) that are equally spaced at two to three meters. The smaller 6 to 10 cm dbh trees tend to be more clumped at less than one to three meters apart. The lower first 6 meter canopy layer contains medium gaps while the third canopy layer (12 meters) contains small gaps. The ravinala palms in this area are 12 meters in height and contribute to canopy layer three. All of the quantified plots for indri group 45 contain small streams except for plot number two.

Indri 45 maximized their use of the heterogeneity in BNR. Indri group 45 used a variety of different patch types, including areas of open and closed canopy of varying heights, pockets of longoza, ridgelines as well as shallow valley areas with streams, and areas with variable densities of small and large diameter trees. The boundary of the indri's range (14.4 ha) (Figure 6.17) bordered the eastern portion of Patch Sahabefoza. The indri in group 45 were separated by Patch Sahabefoza from the other indri groups followed in this research. The indri in group 45 were able to expand their range to incorporate different habitat types without the restrictions from other indri groups and intra-species competition for space and resources. Indri in group 45 occupied the largest home range in comparison to the other radio-collared indri groups. This is interesting because indri group 45 consisted of two individuals that frequently split and traveled, foraged, and rested independently for entire days. The female in this group also incorporated a significant amount of bark into her diet, a behavior not observed to any significant extent among the other lemur

groups[18]. Perhaps there is limited food availability in this area or some nutrient that is lacking in the diet of indri 45 that prompts them to consume more bark. Phenology studies in the future will be important to record resource availability to the indri groups in BNR.

Indri 50

The range occupied by indri group 50 was relatively similar. Five of the seven plots quantified for indri group 50 contained similar counts of 6 to 10 cm dbh trees (13/100 m^2), 11 to 20 cm dbh trees (2/100 m^2), and 21+ cm dbh trees (Range = 3 to 7). The understory tended to be cluttered with a connected canopy. The predominate trees in these plots included hazomainty keliravina and voapaka keliravina. The lower canopy layers in these plots were connected with layer four consisting of small and medium gaps. The one exception to this is plot 5. Plot 5 consisted of a 14 meter tall dying Pallisandre tree growing in an open area surrounded by dead trees and barren understory. The canopy layers had more variation, with small gaps in layers one and two, while layer three was made up of medium and large gaps.

Overall, the plots quantified for group 50 were relatively similar to one another except for plot 7. The main range area consistently used by indri 50 was small (5.4 ha) (Figure 6.17) and relatively similar in structure throughout. Indri group 50's range overlapped extensively with the range of sifaka group 10 and there were two other focal indri groups close by to the northeast and west. Despite the smaller range of group 50, the group was composed of a group of five indri. This suggests a certain level of tolerance for competition in light of this increased group size combined with a homogenized space. The resources must still be abundant in this part of the forest such that indri group 50 can afford to reduce their home range. Perhaps being a folivore allows this type of niche compression (although variability exists discussed further in chapter 7). The indri were often observed to feed on only one or two trees over the course of the entire day. The indri in group 50 showed the highest percentage of resting behavior in comparison to the other groups and also in

[18] Except for indri group 55 that also consumed bark, albeit at a much lower frequency.

comparison to their other behaviors in their activity budget. This suggests the indri may also be adapting behaviorally to their environmental circumstances.

Indri 55

Indri 55 made use of a variety of habitat types. Plot 1 had four canopy layers, all of which were connected, except for the 13 meter fourth layer that consisted of small and medium gaps. Six to 10 cm dbh trees (13/100 m^2) predominated this area with only one 11-20 cm dbh tree and three 21+ cm dbh trees. Plot 1 was dominated by hazontoho trees (N=10). Plot two contained three layers with the third layer largely composed of ravinala palms 15 meters in height. Guava had spread to this area, evidenced by three new plants. Plot two was dominated by maroando (N=12), hazontoho (N=12), and tavolo fotsy (N=19) trees. Plot 3 consisted of a 400 m^2 patch of longoza and open area due to three fallen trees creating a 400 m^2 gap in the forest. The 6 to 10 cm dbh (21/100 m^2), 11 to 20 cm dbh (7/100 m^2), and 21+ cm dbh (10/100 m^2) trees were prominent in this area. The main trees in this plot were lalotina (N=43), maroando (N=39), and tavolo fotsy (N=17). This plot was also near a stream.

Indri 55 used a variety of different patch types, including areas that contained varying canopy layer heights and connectivity, varying densities of different sized diameter trees, longoza and guava patches, and different plant compositions. Indri 55 did not include any of the quantified patches into their range, although the northeastern portion of their range almost bordered Patch Zubenubi. Indri group 55 extended their range further northwest, incorporating a larger amount of heterogeneous habitat into their movement and use patterns. The range (10.1 ha) (Figure 6.17) of indri 55 overlaped slightly with that of sifaka 10. During the all-day follows, the indri and the sifaka were not observed to use the same areas at the same time.

Sifaka 10

Sifaka group 10 incorporated multiple habitat types into its range. In all plots the 6 to 10 cm dbh trees were prominent, ranging in number from 14 to 27, whereas the combined number of

11 to 20 cm and 21+ cm dbh ranged from zero to seven trees. The 6 to 10 cm dbh trees were equally distributed from ≤1 meter apart. In most areas the height of layer one was 4 meters, layer two was 6 meters, and layer 3 was 9 meters. Layers one and two were connected while layer 3 ranged from having small to medium gaps. Plot 1 contained dense lianas (N=22) and the lower 4 to 5 meter canopy layer was the dominant layer. The upper canopy consisted of small and medium gaps. The main trees in this area consisted of mampay (N=20) and tavolo fotsy (N=17). Plot 2 was more of an open space with abundant new growth trees with the larger dbh trees maintaining a clumped spatial distribution. Plot 3 contained a steep rock slope with a 90° drop off and abundant lianas (N=57). This plot also included a small pocket of longoza and 25% bamboo cover, extending from the ground up to 8 meters. There were no dominant tree taxa in this plot. Plot 5 contained larger dbh trees and a low number of lianas (N=7). The canopy was connected and this was the only plot to have a 15 meter canopy. Predominate trees included apanga (N=19), fanjana (N=26), and tsipatika (N=17).

The range (36.0 ha) (Figure 6.17) of sifaka group 10 was the largest in comparison to the brown lemur or indri groups. The large range of the sifaka traversed many different habitat types, including quantified Patch 1600. The range of sifaka group 10 overlaps the ranges of *Eulemur* 34 and indri groups 55 and 50.

Sifaka 1

Sifaka group 1, similar to sifaka group 10, also incorporated multiple habitat types into its home range. The canopy heights in all of the plots were connected except for the fourth layer, which consisted of medium gaps. The canopy heights of all four layers were consistent, including a 4 m, 6 m, 10 m, and 13 m layer. None of the plots contained guava, longoza, or were near streams. Plots 1 to 3 were all located within Patch Fara. Plot 4 consisted of a sharp ridge-line with a 30° drop off on either side. There were large boulders in this area, anchoring the trees. The main trees here consisted of hazomainty keliravina (N=21), vongo keliravina (N=53), and ravinala palms that were

as tall as the 6 meter canopy layer. Plot 5 consisted of a less dense understory composed also of hazomainty keliravina (N=15), vongo keliravina (N=67), and mampay (N=15). The trees in plot 6 were clumped with a spatial distribution of less than one meter to two and three meters. The main trees are hazomainty keliravina (N=19) and maroando (N=15). Sifaka group 1 also incorporated Patch Fara and Patch Sahakoho into their range (23.0 ha) (Figure 6.17). Sifaka group 1 used a range of different habitat types in their movement and use patterns. The sifaka in this group also maintained a large range that facilitated the potential for more habitats to exist within this space.

Macrohabitat Summary

Ultimately, living in a forest fragment affords limited space for the biodiversity. The lemurs have limited places to go in BNR, perhaps forcing them into certain patches. If this is the case, the lemurs are compelled to adapt their behaviors to what is available and therefore may not be choosing a patch because of the structure available. This seems to be the case with the radio-collared brown lemur group and indri groups 14 and 50.

In general, brown lemurs are ecologically flexible in BNR, as was shown with the point counts in this research. However, *Eulemur* group 34 maintained a homogeneous small home range squeezed into a congested part of the forest consisting of tree falls and liana tangles. Other lemur groups often chased these lemurs out of feeding trees or even their path of travel. This brown lemur group may be limited socially and not ecologically, explaining the use of the small space. It is important to note that despite being forced into this cramped space, the brown lemurs adapted to their situation and made do with the substrates available to them in their environment.

Indri groups 14 and 50 may also be confined to certain areas not because of landscape constraints but as a result of social constraints. These lemurs that are constrained into smaller homogenized areas are still flexible in that they make do with the small area and potential limited resources. This small range size does not appear to be an effect of group size. Group 50 was

composed of five members and yet they still utilized a small range. In contrast, indri groups 40 and 45, composed of one and two members, respectively, maintained larger home ranges.

This use of either homogeneity or heterogeneity also speaks to the flexibility of the genus. Indri and brown lemurs within BNR are capable of using a broad range of different habitat types even though some groups utilize homogenous or heterogeneous areas to a greater or lesser degree. Both radio-collared sifaka groups used large ranges that in effect also incorporated more heterogeneity of the landscape into their movement and use patterns. Sifaka are the rarest lemur in BNR. This rarity may facilitate less intra-group competition, allowing the sifaka to utilize large ranges without the effect of social constraints. Sifaka do eat a variety of higher quality foods (Powzyk, 1997) that potentially need be obtained from a variety of different habitat types. This suggests that the heterogeneity resulting from the natural topography of the landscape, but also change influenced from anthropogenic impact, is beneficial to the sifaka in BNR. This heterogeneity may foster the continued existence of such a small population to continue to survive in a forest fragment.

Collectively, the lemur groups followed were not affected by macrohabitat. The lemurs were capable of traversing a number of terrain types and what would appear as potential boundaries (e.g. longoza fields) with no hesitation or difficulty. The only major boundary for the lemurs may be the guava thickets located in the southern portion of the reserve. None of the radio-collared lemur groups ventured into this area, and limited lemur taxa were observed to use this area from the point counts or opportunistic sightings.

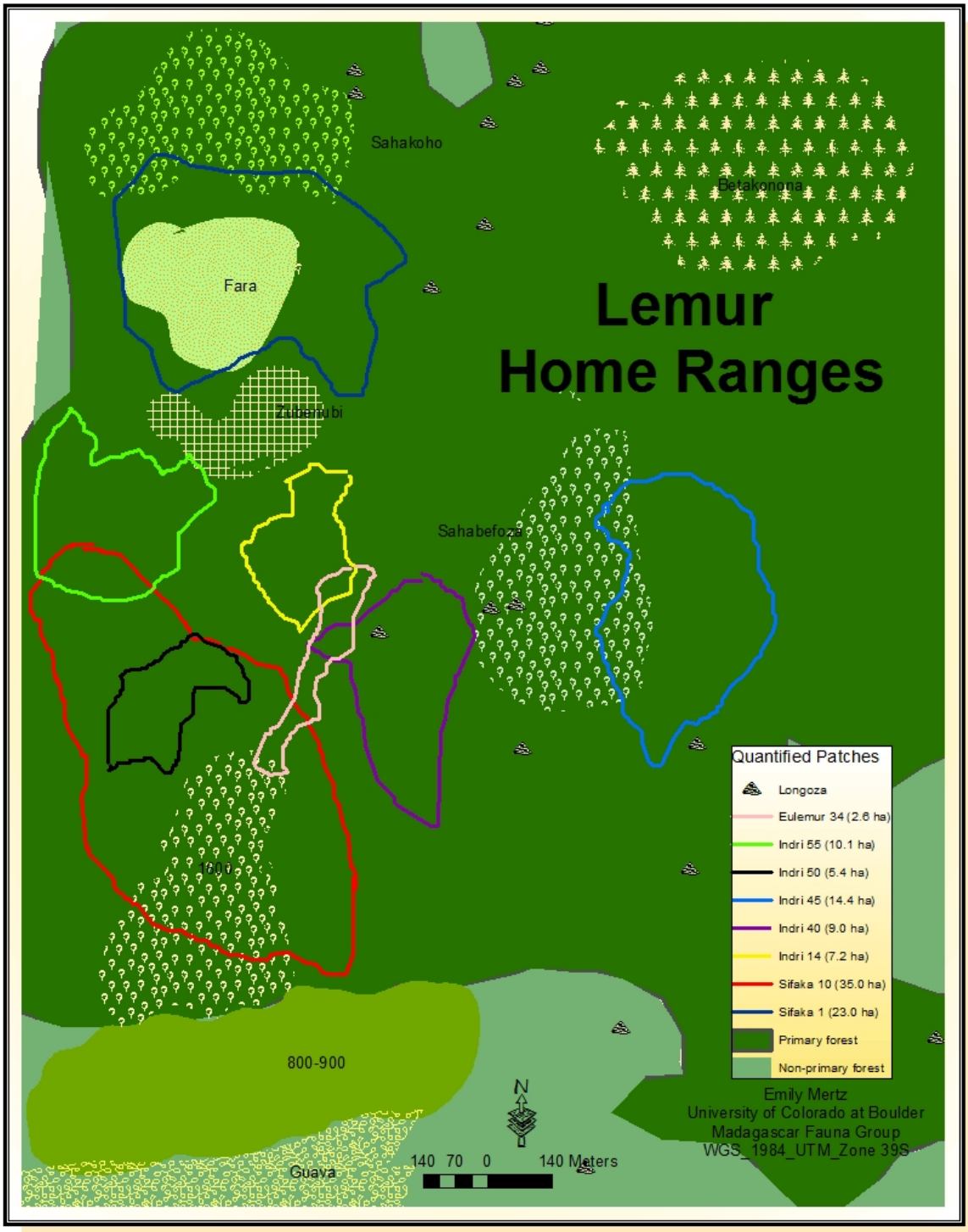


Figure 6.17 Home ranges of the eight radio-collared lemur groups in BNR.

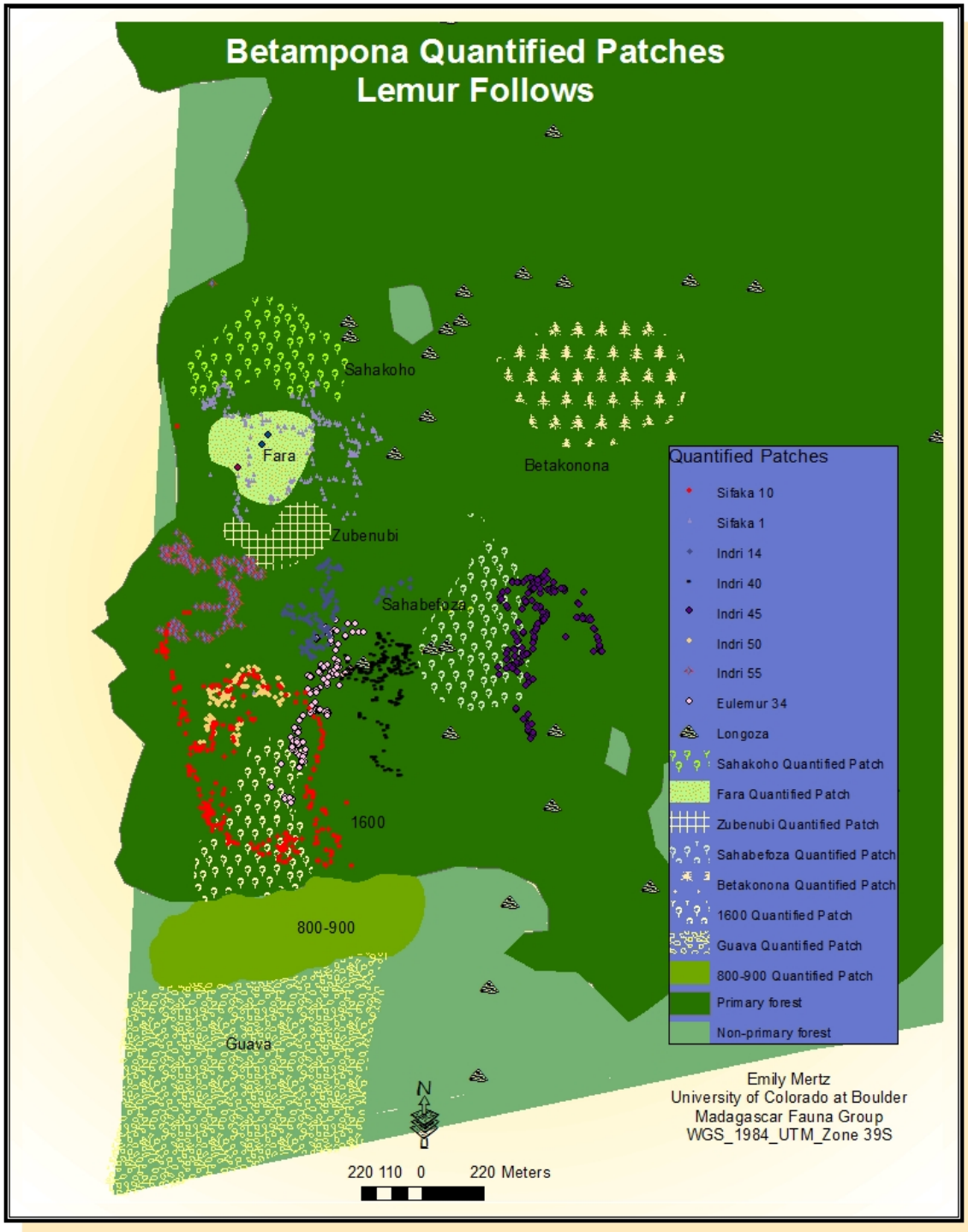


Figure 6.18 Patch use of the eight radio-collared lemur groups in BNR.

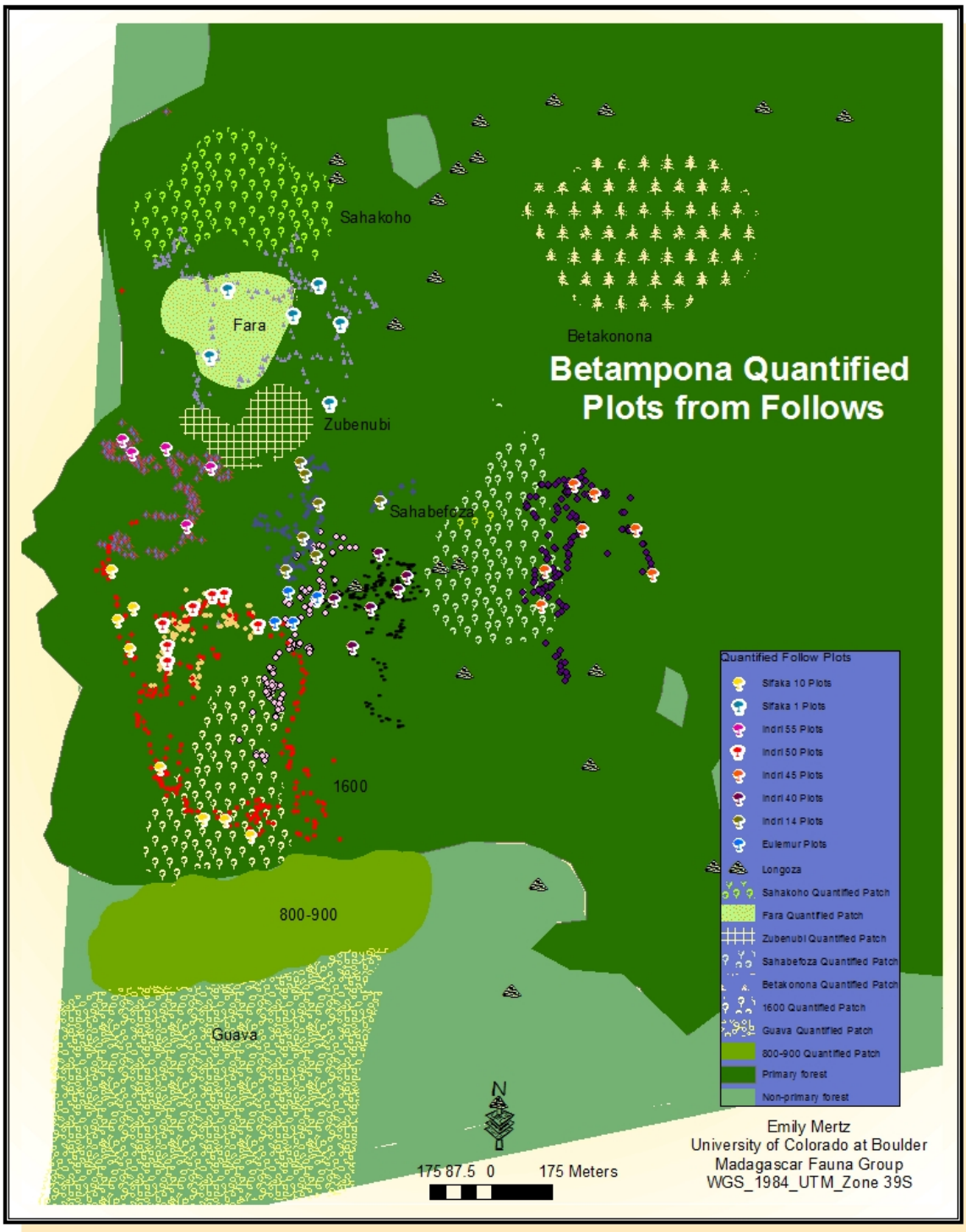


Figure 6.19 Additional quantified plots of the eight radio-collared lemur groups in BNR.

CHAPTER 7
DISCUSSION

Comparison of Methodologies

The objective of this research was to explore the effect of landscape spatial pattern and heterogeneity at multiple scales on lemur habitat use and movement patterns in BNR. To accomplish this goal, eight patches were defined and quantified in BNR that contained distinctive microhabitat and structural vegetative attributes. These patches also represented varying macrohabitat and landscape attributes (e.g. the guava, longoza, or primary forest pattern within or around the patch), which may also be important contributing factors to ecological processes. The purpose of establishing patches in different locations in the reserve was to quantitatively represent the heterogeneity of BNR to ultimately test for the effects of spatial pattern on lemur community occurrence. Moreover, the quantified patches allowed for a certain degree of variable control in an otherwise diverse environment. The dependent variable then, became the lemurs that utilized the patch. Point counts were used in each patch to record which lemurs used the patch and also the behaviors exhibited by the lemur while in the patch[19]. Because it was the patch that was the independent variable and the lemurs the dependent variable, it was only possible to record what the lemurs were doing during the sometimes brief, periods of time while occupying the patch. A complementary methodology was used in tandem with the point counts to account for the full range of habitat use and activity pattern expressed by some of the lemurs. Single individuals within eight different groups of three diurnal taxa were radio-collared and studied by all-day follows. This provided a more robust exploration of daily behavior and the vegetation structure and patch use over the course of an entire day across different months. After a general pattern surfaced of where

[19] The point counts allowed for an assessment of the entire community of five diurnal lemurs. This was important because the radio-collared groups included only three (*Eulemur*, *Propithecus*, *Indri*) of the five. *Varecia* is already part of another long-term re-stocking study and so were not darted (e.g. Britt et al., 2004). We did not have radio-collars small enough to appropriately fit *Hapalemur* in a manner consistent with their welfare. *Hapalemur* were not darted for this research.

the lemurs were going, several plots were established using the same methods as those used for quantifying the eight patches. Although the plots were not as extensively defined as the patches, they still represented the patch type used by the lemur.

There were strengths and weaknesses of both of these methodologies. But used in conjunction, these different approaches overcame the limitations and provided an improved understanding of the interchange between structure and behavior. The use of both methodologies also brought to light some inconsistencies that may occur in the interpretation of the results that depend on the method employed. For example, the indri observed as part of the point counts used three out of the eight patches. This suggests that indri were more limited in the types of patches they used. From a microhabitat standpoint, the indri tended to use patches with a taller canopy and clearer understory. An exception to this is one indri that maneuvered through Patch Zubenubi with no difficulty, making use of the very small substrates and clustered understory. It is important to note that this may have been an anomalous observation and this type of substrate use is not representative of indri. The use of this patch may have been a case of forced occupancy rather than an active choice. Indri are capable of using a variety of substrates if need be, suggesting that microhabitat does not have much of an effect on their patch use. However, patch choice by indri may be driven by certain attributes, indicating that microhabitat is influential.

The observation that indri occurred only in three[20] of the eight patches suggests that the macrohabitat may be more influential than microhabitat in patch choice. This is also an example of the possible difficulty in discerning the greater importance of microhabitat or macrohabitat in driving patch choice. For the indri, is it something about the small-scale features that prevents their use of more patches or is it the landscape features in between? The radio-collared indri groups followed over the course of the day revealed a different pattern. The indri used a variety of different microhabitat features. The indri also were by no means limited by macrohabitat or

[20] If Patch Zubenubi is excluded as a preferentially used patch, then only two patches were used by indri.

perceived landscape boundaries. The indri used a variety of patch types and these differences even extended to intra-group variation. Had only the point count methodology been followed, then the use of a wide range of patch types by indri would have gone undetected.

Eulemur demonstrated another example highlighting the strengths and weaknesses of these methodologies. In general, brown lemurs were ecologically flexible in BNR, as was shown with the point counts in this research. The brown lemurs used all eight of the patches in addition to the area near the perimeter of the reserve and inside the village Rendrirendry near human activity. However, the radio-collared *Eulemur* group maintained a homogeneous small home range squeezed into a congested part of the forest. Here, the radio-collared follow methodology was the limiting factor. It did not fully account for the full range of patch use by *Eulemur*. This brown lemur group was an anomaly in BNR in regards to their patch use, but also in terms of their group size and composition. It is also an important find because it does support the flexibility of *Eulemur*. Despite being forced into this constricted space, the brown lemurs adapted to the substrates available to them in their environment. There are several fruit trees regularly used by the *Eulemur* group in this area that may be important keystone elements, contributing to the successful use of a small range. Moreover, generalist species have been observed to be composed of individual specialists that use a smaller subset of the niche (Durell, 2000; Bolnick et al., 2003). In other words, individuals within a population can vary and may use different resources consequently increasing the niche breadth of a population. An increase in a populations' niche breadth could be achieved in two ways. All of the individuals in a population could shift to exploit a broader resource base or each individual in the population could use a select sub-set of the resources available in the niche thereby decreasing intraspecific competition (Costa et al., 2008). The latter scenario would result in a wider niche breadth because of an increase in among-individual variation (Van Valen, 1965; Costa et al., 2008). Niche variation within a population may help buffer against habitat loss and

subsequent resource loss (Durell, 2000). Utlimately this will provide the genetic variation required to adapt to changing environments (Durell, 2000).

The use of both of the methodologies described above is ideal, especially if a community approach is desired but there are limitations on the number of radio-collared groups. The use of both methodologies in BNR provided a robust tool for the investigation of the synergy between spatial scale and behavior. The following discussion highlights some of the interesting outcomes these methodologies provided with a focus on micro- and macrohabitat features and behavior.

Discussion of Microhabitat

Point Counts

The point counts revealed that microhabitat affected lemur community structure, although the degree to which each lemur taxon was affected varied. Brown lemurs were found in all eight patches, but frequented some patches more than others. Furthermore, the brown lemurs engaged in different behaviors at a higher frequency in some patches, perhaps because of the microhabitat structures. For example, brown lemurs rested more in Patch 800-900. This could be attributed to the abundant 1-5 cm dbh trees, lianas, and dead standing/fallen trees that clutter much of the horizontal and vertical space that provided a protective refuge for the brown lemurs. Brown lemurs regularly slept in these trees during the day but also used them as their overnight sleeping trees. The abundance and diversity of lianas has been observed to increase in areas of disturbance (Laurance et al., 2001) as well as in areas between old growth and secondary forests (DeWalt et al., 2000). *Eulemur* used these dense liana thickets both as a food source, consuming the leaves and the fruits, and as a safe refuge for resting behaviors. *Eulemur* also made use of individual lianas that bridged the gap in open parts of the canopy as important moving substrates. Lianas appear to be important food resources and pathways for brown lemurs. These behaviors have also been

observed in other forest-dwelling animals (e.g. Emmons and Gentry, 1983; Chiarello, 1994; Preece, 2006; Martins, 2009).

The brown lemurs were prevalent in the guava. Although not in bloom, the brown lemurs still relied heavily on the dense guava stands as protective refuge for rest and locomotion. Other sites have also demonstrated the heavy reliance of brown lemurs on guava as a food a source (e.g. Dagosto and Yamashita, 1998).

The point counts revealed that microhabitat also influenced bamboo lemur occurrence. For example, the bamboo lemurs were observed on several occasions to occupy a specific bamboo thicket in Patch 800-900, suggesting this is an important keystone vegetative attribute. The bamboo lemurs moved through a longoza field nearby Patch Sahabefoza to repeatedly use a dense bamboo thicket that existed on the other side in an adjacent patch, indicating another important structure. In Patch Fara, the bamboo lemurs used very small and small-sized lianas in clustered vegetation areas to move and rest at lower heights despite the available tall canopy, open space, and large substrates in this area. These results hint at micro-structure preferences that may determine patch choice by *Hapalemur*.

Based on the point count results, the sifaka groups demonstrated contradictory results. On one hand they did not appear to be affected by microhabitat. While in a patch, sifaka made use of a variety of microhabitat features with no repetitive use of favored trees or their associated attributes and the sifaka were observed to use a variety of patch types. The fact that the sifaka population has not gone locally extinct is remarkable given their very low population size. This perseverance may be attributed to their behavioral plasticity and use of the full range of heterogeneity, both within and between patches, throughout BNR. Sifaka rarity may decrease individual competition within the population thus releasing those individuals from the contraints of intra-specific competition. In turn, this allows the individuals to expand their niche dimensions, or "niche expansion" (MacArthur et al., 1972; Pinka 1994).

The patches that the sifaka were never observed to use during the point counts were Sahabefoza, Zubenubi, and Guava. The Guava and Zubenubi patches both contained abundant low-lying vegetation and liana tangles. This congestion potentially blurred the vertical space for a vertical clinger and leaper, influencing patch choice. These results also suggest, then, that sifaka are affected by microhabitat, and that small-scale attributes may affect patch choice. Taken together, these lines of evidence demonstrate the complexity of determining what really is driving differential patch use. Sifaka residing in the logged forest of Talatakely, Ranomafana National Park, have been observed to consume the guava during certain times of the year (Dagosto and Yamashita, 1998), suggesting the ability to utilize this type of microhabitat. Here, the focus is on landscape ecology and how pattern may affect process, but this still leaves a multitude of other factors (e.g. food availability, hunting pressures, social aspects, territoriality, seasonality) that may be involved in patch choice and habitat use.

In contrast to the sifaka, indri appeared more affected by microhabitat. The two main patches used had a taller canopy and clearer understory. The use of a third patch, Zubenubi, as mentioned prior may not be representative of indri behavior. Furthermore, when indri were observed in this area they tended to remain on the perimeter of the patch feeding and resting in the taller canopy and using the clearer understory to move.

Varecia groups were only observed in one patch, Fara, and seemed to be the most affected diurnal taxon by microhabitat. Fara contained the tallest canopy relative to the other patches. The ruffed lemurs were observed to only use this taller canopy for resting and moving. The ruffed lemurs were not observed to consume any foods while in Patch Fara so the importance or significance of certain feeding trees remains unknown.

Radio-collared Follows

The use of small-scale attributes (microhabitat) and keystone structures were also recorded for the eight radio-collared lemur groups. Because these groups were part of all day follows, a more detailed analysis of their behavior and substrate use was possible. All eight groups were affected by microhabitat features within their resting and moving behaviors. The use of different sized and orientated substrates and associated heights varied among the taxa and even between groups of the same taxon. Furthermore, some groups were affected more than others. For example, the resting and moving behaviors of Lenore, the solitary female, were not affected by substrate size or height. She used a variety of substrates with different attributes in equal proportions of the time. However, Lenore's locomotor modes were affected by the degree of connectivity in the canopy/vegetation. In connected forest she used more one meter leaps and in non-connected forest she focused more so on three and four meter leaps to negotiate the gaps. The level of connectivity in the forest did not affect the locomotor modes utilized by most groups with those lemurs using their full locomotor repertoire regardless of the forest type. This example demonstrates that substantial variability exists, even among individuals, making a definitive single conclusion about the effects of structure and behavior difficult.

The radio-collared lemur groups expressed a heightened preference for some vegetative attributes, which may be driving their patch choice. The radio-collared groups also demonstrated the repetitive use of certain keystone structures for resting, moving, and foraging behaviors. For example, sifaka group 10 used a "liana swing" as an important means of crossing a wide gap in their path of movement caused by a steep decline in the landscape exacerbated by a tree composition composed of low lying apanga palms. The results of the point counts and radio-collared follows methodologies indicate that microhabitat affects lemur behavior, although to varying degrees.

Primates do not use their habitat randomly (Gauthier-Hion et al., 1981; Dagosto and Yamashita, 1998) and appear to not just use supports based on their availability. Research has

documented sympatric species choosing their microhabitat based on structural attributes or floral composition (Harcourt and Nash, 1986; Ganzhorn, 1989; McGraw, 1996). Interestingly, variation exists in species' behavioral responses to differences in structural attributes when comparing habitats. For example, the positional behavior of Verreaux's sifaka (*P. verreauxi*) did not differ significantly in northern and southern study areas in Madagascar, even though the two forests contained structural differences (Richard, 1978). Similarly, Garber and Preutz (1995) found no differences in the positional modes of moustached tamarins (*Saguinus mystax*) due to habitat. But, differences in positional modes were observed among red colobus monkeys (*Colobus badius*) in different habitats at Kibale Forest, Uganda (Gebo and Chapman, 1995). Moreover, a study at two different sites in Ranomafana National Park, Madagascar, found that the positional behavior of the lemurs differed in the two areas, although the responses varied (Dagosto and Yamashita, 1998). The aim of the latter research was to analyze which differences in the structural aspects of the forest affected the positional behavior and substrate use of three lemur species (*Eulemur fulvus*, *Eulemur rubriventer*, and *Propithecus diadema*). This study made a comparison between a moderately disturbed site that included logging, a shorter canopy, and thickets of invasive guava with a forest containing lower levels of logging, a taller canopy, and rarity of guava stands. The results, similar to this research, suggest that positional behavior and support use by lemurs is quite flexible, allowing for a positive response to changes in environmental structure. Dagosto and Yamashita (1998) further elucidate that had their behavioral sampling only taken place in one of the study sites, then a different view would have emerged. The latter emphasizes the importance of sampling behaviors in different parts of a species' habitat range in order to capture the full behavioral repertoire of the study subject. This is particularly important in light of designing corridor projects that need to be extrapolated from a wide base of information of substrates that lemurs (or animals in general) will or will not utilize. Furthermore, we still do not fully understand what features in the forest matter the most to primates. Are primates choosing to use a substrate

first and foremost because of the support size, quadrant availability, canopy connectivity, orientation, or perhaps something even subtler? Building a more extensive database that incorporates habitat use from a variety of habitat types will contribute to answering this question.

Discussion of Macrohabitat

In addition to microhabitat effects, the point counts revealed that the macrohabitat and landscape scales affected lemur community structure. Similar to the microhabitat features, the degree to which each lemur taxon was affected by macrohabitat varied. For instance, Patch 800-900 appeared to be a boundary below which only *Eulemur* and *Hapalemur* were observed to occur. These two taxa were also the only lemurs observed either within the guava or below the guava on the reserve perimeter as well as inside of the nearby village, Rendrirendy. The transitionary forest or the guava thickets were not perceived boundaries for the brown lemurs or bamboo lemurs, taxa that viewed connectivity through this forest characteristic. Perhaps the adjacent patch of 800-900 is deemed poor quality and formed a barrier to the other lemur species studied. The guava produces abundant fruit during certain times of the year; fruit that one might expect to attract frugivores such as the ruffed lemur. However, ruffed lemurs have never been observed in the guava. Perhaps it is due to the adjacent patch, 800-900, that prevents the ruffed lemurs from continuing any further, or the microhabitat of the guava itself that consists of a low canopy and congested understory, or some intricate combination of the different spatial levels. *Eulemur* and *Hapalemur* also used patches that were adjacent to large expanses of longoza fields (e.g. Sahabefoza), even though this macrohabitat feature contributed to a lack of connectivity across the landscape. During point counts, the other diurnal lemurs were not observed to use or move through this patch perhaps due to the perceived barrier of the longoza.

The macrohabitat did not affect movement and habitat use among the radio-collared lemur taxa in BNR. The lemurs were capable of traversing a number of habitat types and what would

appear as potential barriers (e.g. longoza fields) with no hesitation or difficulty. The only major boundary for the lemurs may be the guava thickets located in the southern portion of the reserve. None of the radio-collared lemur groups ventured into this area similar to what was observed from the point counts or opportunistic sightings. Some groups do appear confined to certain areas but this may be better explained as a result of social rather than landscape constraints. As mentioned in the first paragraphs of this discussion, the two methodologies used revealed some inconsistencies in lemur patch use. The point counts suggest more limitations on patch use than what was observed from the all-day follows.

Overall, the flexibility observed by the lemur groups allows them to collectively continue to co-exist in this small forest fragment. Despite the limited space in BNR, the fact that it is heterogeneous space compensates for the small area and allows for a total of eleven lemur taxa to co-exist in this forest fragment. Not only is there heterogeneity within the patch both vertically and horizontally, there is also heterogeneity between the patches, supporting an abundance of biodiversity in BNR. Species-area relationships are often used to evaluate the loss of biodiversity (Ney-Nifle and Mangel, 2000) however; area by itself cannot always explain the decline of some populations in a satisfying manner (Matias et al., 2011). The presence of more species in heterogeneous landscapes may be better explained by the presence or absence of particular types of sub-habitats and not just by patch size alone (Matias et al., 2011). Heterogeneous environments maintain more species diversity than homogeneous ones, allowing for species co-existence, although negative heterogeneity-diversity relationships appear to be more common at smaller scales (e.g. Tamme et al., 2010). The structural variability that accompanies heterogeneity in the environment and the subsequent resource availability can then affect the distribution of different species (Tews et al., 2004). Thus, a reduction in habitat diversity is likely to also result in a reduction in species assemblages (Mckinney, 1998; Hanski, 2005).

In sum, different scales of landscape pattern and heterogeneity affect the various lemur taxa and even single groups and individuals within the same taxon differently. Moreover, the methodology employed may indicate a higher importance of microhabitat or macrohabitat on different lemur taxa and groups. The point count results of this research suggest that micro- and macrohabitat scale features affect lemur behavior, whereas radio-collared follows indicate that macrohabitat has much less of an effect on lemur behavior than microhabitat attributes. Another important outcome of this research is the confounding affect of a social component on lemur behavior and patch use. It appears for example that, some lemur groups may be limited socially rather than ecologically in what patches they use. The complexity of primate social behavior confounds the isolation of landscape variables and their effect on ecological processes.

Complex Synergism between Behavior, Landscape Pattern, and Ecological Processes

The complexity between behavior, landscape pattern, and ecological processes that emerged from this research is not surprising, considering that conserving animals in non-primary forest is increasingly difficult given the unpredictable interactions between species that are experiencing rapid habitat change (Chapman et al., 2003). For example, some of these interactions can include internal (competitive and predatory interactions) (Irwin et al., 2009) and external factors (edge effects, fire intrusions, selective logging, illegal hunting) (Chiarello, 2003). Because of this, it is difficult to make broad generalizations based on a particular response of one population, or even one group of primates with any degree of certainty. The results from this research are a further example of how multidimensional factors may influence behavior and patch use patterns, population size, and extinction risk in a forest fragment. The various lemur taxa and even groups within the same taxon expressed variation in their responses to micro- and macrohabitat features within BNR. The variation that exists in response to different spatial scales and the associated co-variables (e.g. food distribution, social boundaries), which might also be related to seasonality (e.g.

Dagosto, 1995), creates a complex framework within which to implement effective conservation management.

Grouping this variation into a single category called "fragmentation," as discussed at length in chapter one, further undermines the ability to identify unknown potential correlates of risk. In this sense, the search for a simple cohesive explanation or definition of the cause of variation in population decline and environmental limits on complex biological phenomena may be trivial and unlikely (Chapman et al., 2005). What is important is to focus on the variability we do see among biodiversity in these disturbed habitats and appreciate and document the remarkable ecological flexibility and distinguish it from the overarching theme of "fragmentation". This dissertation focused on the development of detailed methodology framed within a specific set of local circumstances in order to provide data for the development of action plans that will conserve biodiversity. Despite the intent and recognition that this type of study is essential to understand the ecological processes that allow the persistence of some primate taxa over that of others in anthropogenically modified landscapes, it is still difficult to explain why some species have higher thresholds of environmental change and thus fare better in forest fragments. If anything, this detail created even more possible variable combinations given the diverse behaviors observed in the lemur taxa, groups, and individuals, amplifying the complexity of biodiversity. Moreover, the comprehensive analysis of vegetation structure and lemur behavior in BNR does not beget general predictions of the effects of structure on lemur behavior. Through a series of examples, the following paragraphs discuss how even the most logical predictions do not always prove general. As discussed in chapter one, there are several variables that may act as indicators as to why some species do better than others in small fragments. The following examples focus on the variables of home range size and degree of frugivory.

Logical Predictions do not Always Prove General: Home Range and Degree of Frugivory

Animals that require large home ranges are unable to persist in small forest fragments because individuals will not be able to acquire the resources needed for survival (Lovejoy et al., 1986; Estrada and Coates-Estrada, 1996). In contrast, animals that have smaller home ranges are predicted to be able to persist in a small forest fragment because they have access to required resources (Lovejoy et al., 1986; Estrada and Coates-Estrada, 1996). A second characteristic suggested to predict survival in a small forest patch is the amount of fruit required in the animal's diet. The uneven distribution of fruits through time and space in comparison to leaves, suggests that frugivores are more likely to be affected by diminishing forest fragments since they require larger home ranges to acquire ample fruit resources (Milton and May, 1976). A classic comparison between howler monkeys and spider monkeys supports this character prediction. The howler monkey (*Alouatta palliata)*, a folivore, and the spider monkey (*Ateles geoffroyi)*, a frugivore, persist in forest fragments in southern Mexico but do not respond equally to environmental change (Estrada and Coates-Estrada, 1996). Groups of *A. palliata* were found to be capable of existing in very small fragments perhaps due to their ability to survive on leaves and maintain a small home range (Estrada and Coates-Estrada, 1996). In contrast, *A. geoffroyi* was not capable of persisting in restricted habitats perhaps due to the large home range required to access sufficient fruit resources to survive (Estrada and Coates-Estrada, 1996). However, this prediction is not absolute. For example, Onderdonk and Chapman (2000) found no relationship between home range and the ability to live in fragments outside of Kibale National Park, Uganda. In fact the study found no clear patterns between any species characteristics (i.e. home range, body size, group size, or degree of frugivory) across the primate community (*Colobus guereza, Cercopithecus ascanius, Procolobus pennantii, Pan troglodytes, Cercopithecus mitis, Lophocebus albigena*) and the ability to persist in a forest fragment. Further, at Lope, Gabon Tutin et al. (1997) found that several frugivorous species were at similar or at higher densities in forest fragment populations compared to continuous forest

populations. Furthermore, diet and home range size can vary among species that reside in continuous forest versus forest fragments. For example the Tana mangabey (*Cercocebus galeritus*) residing in the fragments of the lower Tana River in southeastern Kenya, has been reported to increase its home range size depending on resource availability (Weiczkowski, 2005).

In contrast to frugivores, folivores are predicted to cope with and actually prosper in forest fragments because of the abundance of leaves and edge effects. The edge of a forest fragment maintains a different microclimate than the forest interior. This microclimate results from an increase in sunlight and wind penetration (Murcia, 1995; Laurance, 2001). The new light and climatic conditions stimulate the growth of secondary vegetation. These species produce high amounts of young leaves that typically have fewer chemical defenses, are more digestible, and have higher nutritional value (Ganzhorn, 1992; Ganzhorn, 1995). In addition, less seasonal lianas are more pronounced along forest edges providing a constant food supply (Putz and Windsor, 1987; Morellato, 1996). Folivorous species such as howlers can take advantage of the increased supply of high quality new leaves that are a result of the fragment edge or lightly logged forests (Chiarello, 1994; Crockett, 1998). Therefore, species of the genera *Alouatta* appear to cope with environmental change and are capable of surviving in small patches due to the increase in potential food resources (Estrada et al., 1999; Bicca-Marquez, 2003).

However, *Alouatta* may not be completely immune to the potentially detrimental effects of living in small forests. Brown howlers were found to be extremely rare throughout the forest fragments of Northern Espirito Santo, Brazil (Chiarello and Melo, 2001). Moreover, in a literature review focusing on the effects of habitat loss, fragmentation, and disturbance on howler monkeys (*Alouatta*), Arroyo-Rodriguez and Dias (2010) proposed that habitat loss might have a consistent negative effect on howler populations, indicating that patch size is an important factor in constraining populations. The size of the patch was related to a decrease in the density of big trees, plant species richness, and howlers' home range size. Despite the fact that howlers are one of the

most well studied primates in forest fragments (Estrada et al., 2006), it is still unclear which vegetation attributes have the greatest influence on howler populations (Arroyo-Rodriguez and Dias, 2010). Vegetation composition and structure may be related to patch size, shape, and isolation of the fragment, requiring research designs that permit separation between the effects of habitat spatial patterns and those of vegetation structure (Arroyo-Rodriguez and Dias, 2010). This is needed in different habitat types and landscapes as howler monkey responses to environmental alteration are expected to vary (Ewers and Didham, 2006; Arroyo-Rodriguez and Dias, 2010).

A second example demonstrating the difficulty of generating broad generalizations, that logical predictions do not prove general in all situations, and the complexity of biological systems is illustrated by the red colobus (*Procolobus badius*) and the black and white colobus (*Colobus guereza*) populations that reside in the forest fragments on the periphery of Kibale National Park, Uganda. A census was conducted in 1995 of the primates residing in the forest fragments (Onderdonk and Chapman, 2000). Black and white colobus were found in 17 of the 20 fragments, whereas red colobus were found in 11 of the fragments. This discrepancy was attributed to the dietary diversity required by red colobus. At first, one might predict that having a diverse diet is beneficial. Red colobus would have more food resources to choose from and the probability of finding these resources in a given fragment would be high. However, a consistent diversity of plant species and parts needed over a short period of time may actually be detrimental in that the forest fragment may not provide the diversity needed for survival (Onderdonk and Chapman, 2000). This hypothesis could explain the difference in colobine abundance. Black and white colobus have a relatively "monotonous" diet and may fare better when faced with decreased food availability compared to red colobus that require a diverse diet on a daily basis (Onderdonk and Chapman, 2000). However, a census conducted five years later in 2000 revealed that the black and white colobus population declined by 30% and the red colobus population increased and groups were found in four more of the fragments compared to the 1995 census (Chapman et al., 2003). It was

hypothesized that perhaps the red colobus were moving into the fragments from "overflow" of the continuous forest. Yet, a census conducted in 2003 on the red colobus revealed that the population had declined (20%) once again and groups were limited to 9 fragments (Chapman et al., 2006). This reduction in population numbers was attributed to an increased rate of forest loss that resulted in a decrease in food trees and an increase in parasitic infections (Chapman et al., 2006). This suggests that the red colobus population decreased with the number food trees. This important result runs in opposition to the prediction that food resources (i.e. leaves) are always abundant for folivores (Chapman et al., 2006). This example also demonstrates that the present characteristics of a forest patch that are quantified by a primatologist in one field season may not be strong indicators of primate species responses in the long term.

Thus, it is important to acknowledge the time lag that potentially exists in changing environments and the different species' responses. Understanding the variation observed among species and the changing environment can be infinitely complicated as demonstrated in the above example, and this is but one example in one forest on two species of primates. The variability that exists in determining primate abundance clearly demonstrates that using an all-encompassing term like "fragmentation" trivializes complex biological phenomenon. Presently, "there are few generalizations that work across primate taxa to predetermine success or failure in a fragment" (Marsh, 2003:6). Nor should we try to make generalizations. Great precision is needed on the type of destruction in each particular situation. Environmental conservation endeavors are only suitable in specific places at specific times. This emphasizes the importance of environmental contextualization (Haila, 1997, 1999b).

The results of this dissertation are a further example of the difficulty of making broad generalizations. First, the recommendation for a human-made corridor based on the movement patterns of the eight radio-collared groups is an estimate based on the information from one field season from only eight lemur groups. BNR is a forest comprised of eleven lemur species and a

tremendous amount of non-primate biodiversity. Based on the inter-group variation that exists within a given taxon, it is a daunting task to reduce what lemurs "do" to a couple of variables. Plus, it is difficult to discern the motivation behind the movement patterns of an organism (Lima and Zollner, 1996). Even though restoration efforts may proceed with the best of intentions; there is no guarantee that animals will use the physical structure of the new habitat, the "Field of Dreams" model (Collinge, 2009). With the expense of corridor projects there is not much freedom to "start over."

Second, as mentioned earlier, other variables are most likely working in tandem with vegetation structures that determine patch use, making it difficult to isolate the effects of single variables and determine which one is more important or if that importance changes over time. The population sizes of the lemur taxa in BNR are quite different (Table 7.1), suggesting the abundance of a taxon could influence their distribution throughout the patches. Perhaps abundant taxa are found in more patches because there are more lemurs present to spread out, whereas less abundant lemurs would express the opposite pattern. Brown lemurs are the most abundant taxon in BNR and are found in all eight patches in addition to the nearby village around frequent human activity. The brown lemurs follow the pattern one might expect, but the opposite pattern is also experienced in BNR. For example, bamboo lemurs are abundant in BNR but were only observed in three patches, while sifaka are rare in BNR and were observed to occupy five patches.

Table 7.1 Lemurs abundances from BNR from Britt et al., 2003:1547.

Lemur	Abundance*
Cheirogaleus major	rare
Microcebus rufus	abundant
Lepilemur mustelinus	rare
Avahi laniger	common
Phaner furcifer	common
Daubentonia madagascariensis	rare
Varecia variegata	35-40
Propithecus diadema	15-20
Eulemur fulvus albifrons	250-300
Indri indri	~77-147
Hapalemur griseus	~100

*** Rare: sighted on fewer than five occasions since August 1997; Common: usually sighted every month; Abundant: frequent sightings every month (Britt et al., 2003).**

Abundance is sometimes associated with generalist qualities in forest fragments, but perhaps fragments that express heterogeneity at different levels, such as BNR, will shed new light on the likelihood of extinction. Various characteristics of a species that make them more sensitive to the effects of habitat change and thus more prone to local extinction have been proposed (Turner and Corlett, 1996; Davies et al., 2000; Onderdonk and Chapman, 2000; Henle et al., 2004; Viveiros de Castro and Fernandez, 2004; Ehardt et al., 2005). These characteristics include: populations that are small and fluctuate drastically due to "environmental vagaries" and taxa that experience low intrinsic growth rates, maintain a high degree of arboreality, require large home ranges, require a specialized diet (i.e. frugivory), maintain a large body size, express slow life history patterns, and possess moderate dispersal power including the inability to use the matrix (Bierregaard et al., 1992; Fagan et al., 1999; Henle et al., 2004; Mbora and Meikle, 2004). Another variable to add to this list is the response to heterogeneity.

The following paragraphs discuss the variation among the population sizes of the diurnal lemurs in BNR and pending extinction risk within the context of the acknowledged variables, including the proposed variable – response to heterogeneity. Heterogeneity should be included in

our list of variables that effect extinction risk. Many species require more than one type of habitat (Law and Dickman, 1998), as previously discussed in chapter one, and therefore would benefit from a heterogeneous landscape. For a given amount of habitat, a more fragmented landscape would contain a higher level of different types of habitat (Fahrig, 2003). At the community level, a mosaic landscape caused by intermediate disturbance may favor some species (Irwin et al., 2010), but if this disturbance continues to spread, decreasing the level of heterogeneity, those same species may suffer and eventually become locally extinct (Ganzhorn et al., 1997).

Diurnal Lemurs of BNR: Variation in Abundance, Intrinsic Biology, and Response to Heterogeneity

Varecia variegata is usually the first primate to disappear when faced with human-induced habitat loss within its range in Madagascar (Britt, 2002). The heightened sensitivity of *Varecia*, both behaviorally and demographically, to degraded habitat may be the result of their highly frugivorous diet (Britt, 2000; Vasey, 2000; Balko and Underwood, 2005). *Varecia* has an unusual life history for such a large-bodied (2.6-4.1 kg) diurnal lemurid (Vasey, 1997). *Varecia* are seasonal breeders where females are receptive for only a couple days per year (Foerg, 1982). The average gestation length is 102.5 days, but can vary between 100 and 106 days (Foerg, 1982; Rasmussen, 1985). Females give birth to altricial infants with an inter-birth interval of one year (Vasey, 1997). Because females give birth to litters (1-5 each weighing 100 g) and produce altricial young and rich milk, female ruffed lemurs may have high reproductive demands (Overdorff et al., 2005; Tilden and Oftedal, 1997; Vasey, 1997). Moreover, ruffed lemurs develop more rapidly than do infants of other *Lemur* spp. (Klopfer and Boskoff, 1979) and may attain 70% of their average adult body weight by 4 months (Pereira et al., 1987). Ruffed lemurs engage in high maternal investment and may experience a certain degree of stress during reproduction (Young et al., 1990). A combination of prenatal and postnatal energetic investment, a high (64%) infant mortality rate, variation in the birth rate from year to year, and increased foraging during lactation may all influence the high

reproductive stress potentially experienced by females (Simons, 1990). But, given the relatively short gestation period, large litter size, and rapid infant development one could suggest, based on these life history patterns that *Varecia* would be able to recover from mortality caused by habitat loss. However, this does not appear to be the case.

This is important in conservation research as differences in life history traits may provide insight into the ability of certain species to recover from natural and anthropogenic change. Other species are unable to compensate for increased mortality and are therefore more vulnerable to population extinction (MacArthur and Wilson, 1967; Purvis et al., 2000). Furthermore, the individual based traits of growth, reproduction, and survival all influence the rate at which a population renews itself (Kokko et al., 2001). Since the rate of renewal is connected to the sustainability of a resource, individual life history traits are of understandable interest in effective implementation of conservation strategies (Kokko et al., 2001). Intrinsic vulnerability from life history characters may provide indications of different species' vulnerability to habitat perturbation. Although theory predicts that individuals with slower life histories will be more susceptible to a given degree of anthropogenic exploitation, it is important to note that a given species' life history characteristics do not always predict its rarity or abundance. This emphasizes the point that intrinsic vulnerability because of life history is only one factor determining the viability of a population. Therefore, it is critical to consider multiple factors of the interacting community (i.e. ecological, hunting pressures, interspecific competition in effective conservation management). With *Varecia*, fruit availability during critical life history events may affect population density as well as social organization (Balko, 1998; Vasey, 2000). This ecological inflexibility may have contributed to the low population number residing in Betampona, in addition to hunting pressures that *Varecia* faced in the past (Britt et al., 2003a). These hunting pressures may again be on the rise due to the recent coup and subsequent increasing poverty among local

villages surrounding BNR. The increase in bushmeat consumption is certainly accelerating in other parts of Madagascar at this time (e.g. Jenkins et al., 2011).

Varecia was only found in one patch of forest during the point counts. This forest boasted the tallest canopy and highest percentage of old growth forest. The incapacity to use other forest types could ultimately be detrimental to ruffed lemurs in BNR. Surveys in Ranomafana National Park, Madagascar also revealed that *Varecia variegata* was only present in the lightly disturbed primary forest (Irwin et al., 2005; Herrera et al., 2011). *Varecia* has the most specialized ripe fruit diet of all the lemurs in the Ranomafana community (Herrera et al., 2011) where just five fruit trees compose a majority of their diet (Balko and Underwood, 2005). However, some flexibility is observed among the *Varecia* at Manombo in southeastern Madagascar. These lemurs exhibited feeding and behavioral modifications after Cyclone Gretelle destroyed 85% of the canopy cover in the forest (Ratsimbazafy et al., 2002). *Varecia* was observed to compensate its diet with fruit from invasive plants and showed the ability to supplement their diet with other foods, such as fungi.

Propithecus diadema is the rarest lemur in Betampona. The life history characteristics of *P. diadema* make it particularly susceptible to anthropogenic disturbances (Lehman et al., 2006c). The relatively long gestation period and inter-birth interval, high infant and adult mortality, and delayed age at first reproduction contribute to a low net reproductive growth rate (Pochron et al., 2004). Moreover, *P. d. edwardsi* and *P. d. diadema* occur naturally at low densities even when found in protected areas (Wright, 1995). *Propithecus diadema* is one of the largest extant lemurs (5.0-6.0 kg) (Powzyk, 1997) (Female 6.0-6.7 kg, Male 5.6-6.0 kg – this research), is a favorite prey item of the fossa (and humans), is an arboreal vertical clinger and leaper, and can maintain a large home range of up to 100 ha (Lehman and Wright, 2000; Wright, 1995). Although, the home range size does appear to be variable with a certain degree of flexibility. Irwin (2007) calculated the home range of his sifaka groups residing in a continuous forest to be 70 and 80 ha, whereas the groups living in fragments maintained smaller ranges of 20 to 37 ha. The home range sizes of the sifaka

focal groups in this study were also small (36 and 23 ha) and more consistent with the home ranges observed by Powzyk (1997) at Mantadia (33 ha, 3 individuals; 42 ha, 6 individuals) and the fragment groups in Irwin's (2007) study.

The sifaka express seven out of the eight characteristics of extinction risk, yet the population continues to persist in BNR. Despite this list of alarming traits, the sifaka appear to prosper in a heterogeneous landscape. Sifaka maintain an energetically expensive lifestyle that consists of brief resting periods, extensive patrols of their territories, and scent marking (Powzyk, 1997). This active lifestyle requires a diverse diet with a range of plant species that are consumed (Powzyk and Mowry, 2003). Perhaps the heterogeneity that provides a range of habitat types allows for their continued survival. However, the sifaka groups residing in fragments in Irwin's (2007) study subsisted primarily on mistletoe for a larger portion of the year. The limited resource availability combined with female dominance patterns exhibited by sifaka had an effect on the fitness level of males. Males exhibited reduced body mass in the fragment populations because of the female's priority access to food resources. At other sites *Propithecus* spp. demonstrate plasticity in their social behaviors, home range size and fruit consumption (Arrigo-Nelson, 2006; Irwin, 2008) and have equal encounter rates in areas of lightly disturbed primary forest and logged areas (Herrera et al., 2011). Thus, these primates are capable of flexible responses in disturbed habitats.

Eulemur fulvus is the most abundant lemur species in Betampona. *Eulemur fulvus* is ecologically and behaviorally flexible (Overdorff and Johnson, 2003) and are found in almost every forested area of Madagascar (Tattersall and Sussman, 1998). *Eulemur fulvus* is frugivorous and is capable of exploiting over 100 plant species, but can also focus on 5 to 15 plant species each month (Overdorff and Johnson, 2003). Brown lemurs select a variety of foods over the course of a year according to their seasonal or monthly availability, thus accessing foods with consistent quality (Tarnuad, 2006). Furthermore, members of the genus *Eulemur* exhibit cathemeral activity (Tattersall, 1987) where eastern brown lemurs have been observed engaging in activity across 24-

hour periods throughout the year (Rasmussen, 1999). The brown lemurs in BNR are also cathemeral and sometimes had midnight or early morning parties in the fruit trees above my gheet that entailed the throwing of fruit, loud grunts, and daring belly flops onto the roof. What initiates this cathemeral activity is largely unknown, although moon phase, predation risk, food availability, and/or competition have all been suggested as possible explanations (Overdorff and Johnson, 2003).

Eulemur fulvus group size is small consisting of multiple males and females (Overdorff and Johnson, 2003). Group cohesion is tight and groups are territorial protecting home ranges of 10 to 16 ha (Overdorff and Johnson, 2003). The *Eulemur* group in this research was observed to maintain a much smaller home range size of 2.6 ha. Within larger groups, males and females will form dyads more often than members of the same sex (Overdorff and Johnson, 2003). Although the formation of these male-female dyads has been interpreted as pair-bonding (Jolly, 1998) or a "special-relationship" (Pereira and McGlynn, 1997), other research has indicated that these relationships are unstable or uncommon (Overdorff and Johnson, 2003). Brown lemurs give birth almost every year and do not invest as much energy in their offspring during reproduction as other strepsirrhines (Overdorff and Johnson, 2003; Tarnaud, 2006). Females also produce low quality milk that decreases the post-reproductive energetic demand of raising offspring (Tilden and Oftedal, 1995). Thus, the life history characteristics of *Eulemur fulvus* may be a further contributing factor to the ecological plasticity of this genus.

Some *Eulemur* species may exhibit habitat selectivity (Schwitzer et al., 2007). In northwestern Madagascar on the Sahamalaza Peninsula, *E. macaco flavifrons* showed differences in the structures used in primary versus secondary forest fragments. Also, in the secondary forest fragment the lemurs used larger home ranges and occurred at lower densities, suggesting to the researchers that the habitat type was less suitable. However, inter-group variability in home range size may not be a proxy for habitat suitability.

In BNR, *Eulemur* was observed in all eight patches and has been observed using all areas of the reserve, including areas around the perimeter and in the local village, Rendrirendry. The perimeter vegetation of Betampona is characterized by invasive guava and abundant traveler's palm. *Eulemur* individuals benefit from this habitat type because of increased foraging opportunities on the seeds and nectar of the traveler's palm and fruit and leaves of guava. All of the different patch types perhaps allow this large population size of brown lemurs to continue to exist in BNR. There are areas of primary forest, non-primary forest, and all of the variation in-between, allowing a positive response from the brown lemurs. As noted in chapter six, the radio-collared brown lemur group maintained a small range (2.6 ha). The heterogeneity within the patch, in addition to a few keystone fruit trees, perhaps allowed for these brown lemurs to continue persisting in such a small area. Studies of *Alouatta palliata* have shown that home range size decreases with decreasing patch size limiting the amount of resources available to each group (Cristobal-Azkarate and Arroyo-Rodriguez, 2007). However, a small home range does not always result in low food availability (Gillespie and Chapman, 2001), as it is also important to look at the specific structure and composition of the forest fragment (Arroyo-Rodriguez and Dias, 2010).

Hapalemur griseus are small-bodied primates (0.75 – 1 kg) (Tattersall, 1982) and are distinctive among primates in that a majority of their diet consists of bamboo (Tan, 1999). Although *H. griseus* specializes on bamboo, it is capable of subsisting on a diet devoid of bamboo (Mutschler et al., 1998; Mutschler, 1999). Furthermore, *H. griesus* is capable of thriving in degraded habitat and is quite resilient to habitat disturbance (Strier, 1992; Grassi, 2006; Martinez, 2008). *Hapalemur griesus* actually has higher group densities and larger social groups in degraded areas where they have been observed primarily eating invasive species such as guava (Grassi, 2006). *Hapalemur griseus* mainly live in small groups of 2 to 7 and exhibit variable social groupings where either a breeding pair or several breeding females make up the group composition (Tan, 1999). *Hapalemur griseus* are territorial and will defend a 15-20 ha home range (Tan, 1999; 2000).

Hapalemur have a gestation length of 137 days, resulting in a litter size of one (Wright, 1990; Tan, 2000) with an inter-birth interval of one infant per year (Mutscler and Tan, 2003). The intrinsic characteristics of *Hapalemur* in addition to their ecological flexibility may contribute to their persistence and larger population size in BNR.

During the point counts, bamboo lemurs were observed to use three patches. The observation of these lemurs in only three patches may be due to their cryptic nature or fleeing the area upon human arrival and so this number may not be truly reflective of their entire range of patch use. The patches that the bamboo lemurs used however were quite different in terms of their micro- and macrohabitat attributes. This suggests that heterogeneity may be an important factor for the continued survival of bamboo lemurs in BNR. Studies conducted at Ranomafana (e.g. Grassi, 2006) indicate that bamboo lemurs do quite well in areas inundated with guava. Bamboo lemurs were never observed using the guava during this research but the important factor here may be that the guava was not in bloom.

Female *Indri indri* and *P. d. diadema*, are the largest living lemurs (6.48 kg) (Powzyk, 1997) (Female 6.6-8.4 kg, Male 5.9-7.3 kg – this research). Despite this large body size, indri is relatively abundant in Betampona (77-147 individuals) (Glessner and Britt, 2005). The dietary range of *I. indri* (immature leaf specialists) with less dependence on patchily distributed food (Powzyk and Mowry, 2003), as well as the local taboos against hunting *Indri* (although starting to break down, e.g. Jenkins et al., 2011), collectively may contribute to their more elastic response to environmental change, thus favorably influencing the viability of the remaining population that exists at Betampona (Britt et al., 2003).

Despite the relatively large population size, their intrinsic biological characteristics indicate they are unlikely to sustain high rates of external pressures. Indri mothers give birth to one infant every 2 to 3 years (Pollock, 1975; Powzyk, 1997) after a gestation period of 120-155 days (Petter and Peyrieras, 1974; Pollock, 1975). Young sleep with their mother for the first year of life (Petter

and Peyrieras, 1974) but then at an age of 6 months, the mother will move independently of the infant forcing the infant to be more self reliant, including making difficult jumps (Petter and Peyrieras, 1974). Infants have been observed falling 30 feet from the canopy several times a day after poorly negotiating tree gaps (Petter and Peyrieras, 1974). Over the second year of life, the offspring is more distant from his or her mother but still within close proximity compared to other group members (Petter and Peyrieras, 1974).

Indri live in small family groups that consist of two adults with young (Powzyk and Thalmann, 2003). However, in fragmented forests larger group sizes have been reported due to the inability to disperse (Pollock, 1975, 1977; Powzyk, 1997). In addition, at Mantadia an undisturbed forest, *I. indri* was observed to occupy territories of 34 and 40 ha (Powzyk, 1997), whereas in degraded habitat groups occupied 17.7 and 18.0 ha territories (Pollock, 1979). The study groups at Mantadia inhabited relatively undisturbed forest and Powzyk (1997) reported that suitable habitat within the indri groups' range was left unexploited, suggesting that food was not a limiting factor. In BNR, immature leaves are the preferred food for indri, but at times of food scarcity other foods are eaten, including mature leaves, fruits, seeds, and bark (Britt et al., 2002). Indri have also been observed to eat tree bark at Mantadia (*Octea* sp., 2.9% feeding time) (Powzyk, 1997). Two indri groups in my study were observed eating bark as well. The efficient gut morphology of indri and their less active lifestyle, short day range, short active periods, fewer feeding bouts, and focus on abundant leaves allow indri to conserve energy on a daily basis (Powzyk, 1997).

This ecological and social flexibility is also observed among the indri of BNR. The different groups of radio-collared indri expressed group sizes ranging from a solitary female to a group of five. The range size also varied with some groups maintaining ranges much smaller than other groups. In BNR, previous research has recorded home range sizes of 21, 24, and 36 ha of indri focal groups (Glessner and Britt, 2005). These groups also ranged in size from 2 to 5 individuals. In comparison, the indri groups followed as part of my research maintained much smaller home

ranges (5.4 ha to 14.4 ha respectively). Some of these ranges included a variety of habitat types, whereas others were more homogeneous. The indri also demonstrated variability in their behaviors, perhaps as a plastic response to resource availability in their range. For example, indri group 50 contained five members and used the smallest range size. This group of indri also incorporated the highest percentage of resting behaviors into their activity pattern. Indri group 14 contained three group members, also maintained a small range, but this group incorporated the highest percentage of feeding behaviors into their activity budget. These two examples demonstrate there is complicated variability among these indri groups, which requires more in depth research of resource availability in each of their ranges to understand more about the effects of within-patch heterogeneity. The variability that exists within a forest, a species, a group, or an individual suggests that environmental conservation endeavors need to be primarily site specific.

The indri population in BNR is relatively high in comparison to the other diurnal lemurs, but is well below the minimum effective population size for long-term survival[21]. Results from other indri studies in BNR suggest that habitat quality and degradation most likely are influential in determining the population density and range size of different groups (Britt et al., 2002; Glessner and Britt, 2005). In these prior studies, the small ranges occupied by the different indri groups had undergone an intermediate level of disturbance and were bordered on the south and northwest by non-primary forest. An increase in poor "quality" habitat may result in an increase in density plus a decrease in home range size. This could be the case with group 50 in my research. This has also been observed in *Colobus guereza* in Kibale Forest, Uganda, that live at increased densities in logged

[21] In the 1980s the minimum population size for long-term survival was estimated to be around 500 adult individuals (Franklin, 1980). Today there is debate about the applicability of minimum population viability numbers (MVPs). Some researchers argue that long term persistence requires ≥ 5000 adult individuals to "ride-out" environmental fluctuations (Traill et al., 2010). Others argue that there is no "magic number" (Flathers et al., 2011). The variability that exists among species prevents the use of a universally applicable MVP. Flathers et al. (2011) argue that generalizing among species is a dangerous undertaking and can lead to the misdirection of scarce resources delegated to conservation research. Generalized MVPs could also lead to dismissing a population as a lost cause, although still viable, because the numbers are well below the guidelines. Ultimately this could lead to an unstable foundation with which to base conservation decisions.

areas compared to unlogged areas (Strusaker, 1975; Skorupa, 1986) and have decreased home range sizes in smaller forest patches (Onderdonk and Chapman, 2000). Based on the results of their density study on indri, Glessner and Britt (2005) suggest that unoccupied suitable habitat is limited in BNR. Perceived "degradation" requires more detailed phenology studies of the ranges inhabited by indri in BNR.

Quantifying Structure and the Role of Landscape Ecology

In an effort to understand more about the effects of anthropogenic change on biodiversity there is a focus on quantifying structure and habitat use (e.g. Branch, 1983; Terborgh, 1983; Schwarzkopf and Rylands, 1989; Peres, 1993; Wallace et al., 1998; Warner, 2002; Ellwanger and Gould, 2011). However, many of these studies evaluate a stark dichotomy between primary and secondary, logged or unlogged, continuous or fragmented and ignore the heterogeneity that exists within each of these categories or across the landscape (e.g. Dagosto and Yamashita, 1998; Schwitzer et al., 2007; Boyle and Smith, 2010; Chagas and Ferrari, 2010; Link et al., 2010; Moore et al., 2010; Pyritz et al., 2010; Chavas and Stoner, 2011; Herrera et al., 2011, Hardus et al., in press). Secondary and degraded forests and all the variation in between should be important in conservation initiatives. These types of forest provide crucial habitat for a variety of species (e.g. Dent and Wright, 2009). Moreover, non-primary forest now comprises as much as 60% of the world's remaining forest and 42 tropical countries report a higher percentage of degraded forest than primary forest (FAO, 2006). A focus on non-primary forest and landscape mosaics will be an important focus for conservation initiations in these countries (Dent and Wright, 2009).

The effects of the breaking-apart of the landscape and consequent heterogeneity independent of habitat loss have received little attention within primate research. The goal of this study was to establish a spatial framework with detailed vegetation structural analysis of a forest fragment to facilitate research concerning movement and differential patch use among lemurs. This

type of analysis allowed for the assessment of the spatio-temporal variability in the distributions, productivity, and survival of lemurs in a heterogeneous forest fragment. The results indicate that quantifying variation in habitat use across the landscape and identifying habitat structural variables and patterns at micro – and macro – level scales was important to understand the influences of variation among primate assemblages in different habitat types. A complex view of habitat use, sociality, and scale also became apparent in light of the radio-collared lemur groups. Ecological and social complexities suggest that general statements about extinction risk are unproductive to make in some instances. This does not necessarily mean, however, that detailed ecological and behavioral data sets are unimportant. Compiling information on site-specific habitat use will impact conservation policy by contributing much-needed data sets for informed decisions pertaining to land development based on species habitat preferences and movement patterns, where to restore habitat, where to protect habitat, and where to build/maintain connectivity.

Landscape ecology makes use of integrative methods that allow for the identification, analysis, and synthesis of complex natural and cultural patterns and processes on different spatial scales. The three-dimensional effects of spatial heterogeneity on biodiversity can be revealed through collecting detailed data in integrated field surveys, GIS, and remote sensing that collectively can be used to see changes over time. Yet, even detailed accounts of habitat use, behavior, and movement patterns reveal that biodiversity is complex, requiring thoughtful discussion of the variables synergistically involved. Grouping this complexity under an umbrella term like "fragmentation" prevents the ability to discern where the risks truly lie and ultimately the development of accurate conservation planning. There is a need then, to turn semantics into pragmatic conservation action. Given the growing focus on fragmented landscapes as anthropogenic and natural processes continue to threaten tropical forests worldwide, we need to be more specific in our discussion of accurately reporting complex ecological processes and biological idiosyncrasies. It is this attention to detail framed within a specific set of local

circumstances that will conserve biodiversity, not the verbal and written use of an "intellectual attractor" (*sensu* Villard, 2002). The application of landscape ecology, coupled with conventional forest fragmentation research, to the conservation of primates creates an opportunity to expand the methodologies of the anthropological study of primates, particularly as it relates to patterns of extinction, anthropogenic alteration of habitats, and the human effort to conserve irreplaceable resources.

Conclusion

The goal of this research was to understand how the context of landscape spatial pattern relates to lemur behavioral and movement processes in a forest fragment. The distinctive ecology of BNR provided an ideal situation to understand in more detail the effects of landscape modification and heterogeneity on lemur community structure. The results indicate that there are quantifiable differences between the patches within BNR. These patches demonstrate differences in microhabitat as well as macrohabitat attributes of the internal patch and surrounding area. The results also indicate that there are differences in diurnal lemur community structure within the quantified patches of BNR. Different scales of landscape pattern and heterogeneity affected the various lemur taxa and even single groups and individuals within the same taxa differently. Certain microhabitat features appeared to be important keystone structures to different lemur taxa, which might drive patch use. The point count data also revealed that macrohabitat was a factor contributing to differential patch use. These data suggest that the use of different patches by the lemurs was contingent upon the perceived quality of the adjacent patch. Results from the radio-collared follows revealed that microhabitat had a greater effect on lemur patch use than macrohabitat. The lemurs expressed an affinity for particular substrates while in a patch, but demonstrated no environmental barriers while moving through the forest. A more influential barrier might be social rather than ecological.

The consideration of an organism-focused view of heterogeneity was important. The environment could be perceived as unsuitable habitat to the researcher, but the organism may focus on the structural integrity of the habitat regardless of the broad generalizations of "primary" versus "secondary" or "degraded" forest made by the researcher. The lemurs were observed to use a variety of habitat types regardless of the perceived categories. Quantifying the variation in lemur habitat use across the landscape and identifying habitat structural variables and patterns at a micro – and macrohabitat level was shown to be an important component in understanding the primate community assemblages in different habitat types throughout BNR.

The data pertaining to lemur habitat use, important keystone structures, movement patterns, and GIS visual models were given to the Madagascar Fauna Group. The establishment of such a spatial framework, with detailed vegetation structural analysis of a forest fragment, facilitates continued research concerning movement and differential patch use among biodiversity. This framework allows the assessment of the spatio-temporal variability in the distribution and survival of different organisms in the fragmented landscape of BNR. These data will help inform effective conservation management and will be used as a baseline framework from which future research will continue to build. The GIS database has the capacity to incorporate other species data from research in BNR to generate a holistic assessment of ecosystem sustainability. Given the complexity of the rainforest ecosystem of BNR and the need to understand the changing intricate patterns and relationships of such a system over time, the continued development of such a database is urgent to avoid "emergency conservation" so that informed adaptive management may be implemented to meet human needs and the needs of biodiversity. Understanding and predicting the impact of human behavior and modification on biodiversity is increasingly important to our future survival and of ecosystems as human activity dominates an amplified proportion of interactions in ecological communities.

Summary Points

1. There are quantifiable differences between the patches within BNR. These patches demonstrate differences in microhabitat as well as macrohabitat of the internal patch and surrounding area.
2. There is variation in diurnal lemur community structure and diversity indices within the quantified patches of BNR. The most diversity was observed in Patches Fara and Betakonona with the least diversity in Patch Guava. The species evenness (average proportion of the total of each species squared) generally followed Simpson's D for each patch with the more diverse patches also expressing more species evenness.
3. Different scales of landscape pattern and heterogeneity affect the various lemur taxa and even single groups and individuals within the same taxon differently.
4. The research methodology employed may indicate either a higher importance of microhabitat or macrohabitat on different lemur taxa and groups. In this research, the point count results suggest that micro- and macrohabitat scale features affect lemur behavior, whereas radio-collared follows indicate that macrohabitat has much less of an effect on lemur behavior and movement than microhabitat attributes.
5. It is inappropriate to make broad generalizations based on a particular response of one population, or even one group of primates with any degree of certainty. The results from this research are a further example of how multidimensional factors may influence behavior and patch use patterns, population size, and extinction risk in a forest fragment. The variation that exists in response to different spatial scales and the associated co-variables (e.g. food distribution, social boundaries) creates a complex framework within which to implement effective conservation management.

6. Grouping complex ecological and behavioral variation into a single category called "fragmentation," undermines the ability to identify unknown potential correlates of extinction risk.

Future Research

This research has generated additional questions and ideas for future research projects. The results indicate that many of the quantified patches included a variable number of trees of economic value. A patch with a high abundance of trees with economic importance, that are also vital to lemur survival, might have a higher risk factor than a patch with few trees of economic value. In the future, research initiatives will focus on the importance of each of these valuable trees to local communities to more accurately assess the risk factor for each patch. These data sets could indicate pending ecosystem collapse and provide information for a more effective action plan for both conserving biodiversity and the sustainable harvest of forest resources. With a human growth rate of 2.9%, Madagascar has one of the fastest growing populations of countries that possess rainforest (Golden, 2009; CIA World Fact Book, 2012). Additionally, Madagascar is facing economic difficulties that place considerable strain on the forests. People that live alongside the forest and depend on its resources need to be consulted on sustainability initiatives. Legal protection of the animals and plants without the endorsement of local people cannot generate successful conservation action plans.

Furthermore, future research will focus on the understudied community of the six nocturnal lemurs of BNR and their patch use and movement patterns. Facilitating effective corridor designs for nocturnal animals is also important for conservation planning. Phenology studies will also be conducted to address in more detail the importance of resource availability and patch quality. Additional field seasons will address questions pertaining to the role that seasonal variation in resource availability plays in perceived patch quality and use. This analysis will also include the seasonal guava bloom. In addition, I will explore more combinations of positional modes and

substrate attributes with an aim to reveal the subtlety with which lemurs choose and utilize patches. More patches will be quantified to allow a more extensive landscape view of habitat use.

Madagascar's forests are disappearing. The amount of rainforest in Madagascar has decreased the most relative to other forest types, with 40% cleared between 1950 and 2000 (Harper et al., 2007). If the rate of forest loss continues at 150,000 hectares per year, then the primary vegetation of Madagascar will all be lost by the year 2067 (Moat and Smith, 2007). Evaluating the prospects of biodiversity that remain in these small isolated forests is central to conservation management in Madagascar.

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APPENDIX

RESULTS FROM 2007 LITERATURE REVIEW

Species	Topic/Response variable	Study
Lemur catta Androy, Madagascar	Spatial aspects of resilience	Bodin and Norberg (2007)
Avahi laniger, Cheirogaleus major, Lepilemur mustelinus, Microcebus rufus, Eulemur rubriventer, Eulemur fulvus rufus, Eulemur fulvus fulvus, Propithecus d. edwardsi, Varecia variegata Fandriana-Marolambo, Madagascar	Ecological correlates to lemur community structure	Lehman et al. (2006)
Procolobus rufomitratus, Cercocebus galeritus galeritus Tana River forest, Kenya	Population trends	Wahungu et al. (2005)
Colobus vellerosus Boabeng-Fiema Monkey Sanctuary, Ghana	Habitat quality and diet	Wong et al. (2006)
Alouatta seniculus Lago Guri, Veneuela	Indirect interactions of howler monkeys and bird richness	Feeley and Terborgh (2006)
Procologus badius temmincki Fathala Forest, Senegal	Behavioral adaptations	Galat-Luong and Galat (2005)
Colobus vellerosus Boabeng-Fiema Monkey Sanctuary, Ghana	Population size and density	Wong and Sicotte (2006)
Cercopithecus mitis Lophocebus albigena Kibale National Park, Uganda	Densities of frugivious primates with respect to forest and fragment tree species composition	Worman and Chapman (2006)
Alouatta palliata Los Tuxtlas, Mexico	Diet and activity pattern	Cristobal-Azkarate and Arroyo-Rodriguez (2007)
Alouatta palliata Los Tuxtlas, Mexico	Indirect interactions of howler moneys and dung beetles	Estrada et al. (1999)
Piliocolobus tehrosceles Kibale National Park, Uganda	Food availability and stress impacts on populations	Chapman et al. (2006)
Colobus angolensis palliatus Kwale District, Kenya	Matrix use	Anderson et al. (2007)
Mico Argentatus Para, Brazil	Genetics/patch size	Goncalves et al. (2003)
Colobus guerza, Cercopithecus ascanius, Colobus pennantii, Pan troglodytes, Cercopithecus mitis, Lophocebus albigena	Population size/metapopulation dynamics	Chapman et al. (2003)

Kibale National Park		
Alouatta palliata Southern Veracruz, Mexico	Demography/behavior	Rodriguez-Toledo et al. (2003)
Allouatta fusca, Cebus apella, Callicebus persoantos, Callithrix geoffryoyi Brazilian Atlantic Forest	Density of primates in various sized forest fragments	Chiarello (2003)
Aotus infulatus, Cebus apella, Saimiri sciureus, Mico argentatus, Alouatta belzebul, Ateles belzebul, Ateles marginatus, Callicebus moloch, Chiropotes albinasus Para, Brazil	Primate abundance/fragment size.	Ferrari et al. (2003)
Alouatta seniculus, Ateles panisus, Cebus apella, Chiropotes satanas, Pithecia pithecia, Saguinus midas Biological Dynamics of Forest Fragments Project, Amazon Basin	Primate abundance and fragment size	Gillbert (2003)
Macaca silenus, Trachypithecus johnii Western Ghats, India	Abundance/demographic parameters and fragment size/quality	Umapathy and Kumar (2003)
Ateles geoffroyi Punta Laguna, Mexico	Population size and habitat use	Ramos-Fernandez and Ayala-Orozco (2003)
Alouatta seniculus, Cebus nigrivittatus, Pithecia pithecia, Chiropotes satanus	Comparison of forest structure and plant species composition on an island	Norconk and Grafton (2003)
Species	**Topic/Response variable**	**Study**
Alouatta palliata mexicana Agaltepec Island, Vreacruz, Mexico	Foraging strategy	Rodriguez-Luna et al. (2003)
Genus Alouatta Cross site comparison	Ecology and behavior predicted by fragments size	Bicca-Marques (2003)
Pan troglodytes schweinfurthii Masindi District, Uganda	Sugar cane/human-primate conflict	Reynolds et al. (2003)
Alouatta seniculus, Saguinus midas, Pithecia pithecia Manaus, Amazonas, Brazil	Habitat quality and structural diversity	Schwarzkopf and Rylands (1989)
Presbytis melalophos, Macaca nemestrina, Hylobates lar, Macaca fascicularis Peninsular Malaysia	Emphasis on habitat loss, habitat quality	Laidlaw (2000)
Hylobates hoolock, Trachypithecus pileatus, Macaca mulatta, Macaca assamensis,	Emphasis on habitat loss	Srivastava et al. (2001)

Macaca nemestrina, Nycticebus coucang Borajan Reserve Forest, India		
Callithrix aurita Mata da Olaria, Brazilian Atlantic Forest	Feeding ecology and habitati loss	Martins and Setz (2000)
Cercocebus galeritus sanjei, Procolobus badius gordonorum, Colobus anolensis palliates, Cercopithecus aethiops, Papio cynocephalus, Otolemur crassicaudatus, Galago senegalensis, Galagoides orinus, Galagoides udzungwensis Udzungwa Mountains, Tanzania	Distribution and status	Dinesen et al. (2001)
Cercocebus galeritus galeritus Tana River, Kenya	Population viability	Kinnaird and O'Brien (1991)
Trachypithecus leucocephaus China	Distribution and status	Huang et al. (2002)
Propithecus verreauxi, Eulemur fulvus, Lepilemur ruficaudatus, Phaner furcifer, Mirza coquereli, Cheirogaleus medius, Microcebus murinus, Microcebus myoxinus Morondava and Kirindy Forest, Madagascar	Forest regeneration	Ganzhorn et al. (1999)
Brachyteles arachnoids, Cebus apella nigritus, Alouatta guariba clamitans Paranapiacaba, Atlantic Brazilian Rainforest	Primate density, absence of top predators, ecological plasticity	Gonzalez-Solis et al. (2001)

Species	Topic/Response variable	Study
Alouatta palliata Chiapas, Mexico	Distribution and abundance as a function of patch quality and connectivity	Anzures-Dadda & Manson (2007)
Alouatta palliata Los Tuxtlas Special Biosphere Reserve	Analyzed changes in howler habitat, availability of plant families.Fragment size was the variable that best explained variation veg comp and stucture.	Arroyo-Rodriguez & Mandujano (2006)
Alouatta pigra Palenque, Chiapas, Mexico	Forest loss and troop size, age, and sex composition	Estrada et al. (2002)
Alouatta fusca, Cebus apella, Callicebus persoantos, Callithrix geoffryoyi Northern Espirito Santo, Brazil	Assessed population densities.Numbers higher in larger than smaller fragments.	Chiarello and Melo (2001)
Ateles spp., *Alouatta* spp., *Callithrix* spp., *Callicebus moloch, Cebus apella* Alta Floresta, Brazilian Amazonia	Persistence of primate and carnivore assemblages	Michalski & Peres (2005)
Callithrix jacchus Atlantic Forest, Brazil	Population surveys	Mendes-Pontes et al. (2007)
Macaca silenus Indira Gandhi Wildlife Sanctuary	Changes in time budget and feeding ecology with reference to area and vegetation status	Umapathy and Kumar (2000)
Alouatta caraya Northern Argentina	Density and social organization	Zunino et al. (2007)
Colobus guerza, Cercopithecus ascanius, Colobus pennantii, Pan troglodytes, Cercopithecus mitis, Lophocebus albigena Kibale National Park, Uganda	Species in patch, tree species composition, area of patch, and distance to nearest patch	Onderdonk and Chapman (2000)
Cercocebus galeritus Tana River, Kenya	Ecological correlates of abundance of mangabeys	Wieczkowski (2004)
Colobus guereza, Cercopithecus ascanius 'Kampala area', Uganda	Abundance, patch quality, and patch size	Baranga (2004)

Propithecus d. diadema Tsinjoarivo, Madagascar	Group cohesion and food resources	Irwin (2007)
Procolobus rufomitratus Tana River, Kenya	Habitat factors that determine occurrence	Mbora and Meikle (2004)
Cheirogaleus major Vohibola III Classified Forest Madagascar	Edge effects on density	Lehman et al. (2006)
Avahi laniger, Cheirogaleus major, Eulemur rubriventer, Hapalemur griseus griseus, Microcebus rufus, Propithecus d. edwardsi Vohibola III Classified Forest Madagascar	Edge effects and lemur responses	Lehmaan et al. (2006)
Propithecus tattersalli Daraina region Madagasacr	Distribution and conservation status	Vargas et al. (2002)
Gorilla .g gorilla, Pan t. troglodytes, Mandrillus sphinx, Colobus satanus, Cercocebus albigena, Cercopithecus nictitans, C. pogonias, C. cephus Lope, Gabon	Behavioral ecology of primates in continuous forest versus fragment	Tutin (1999)

FREQUENTLY USED TREES BY LEMURS FROM ALL DAY FOLLOWS

SIFAKA GROUP 1 FREQUENTLY USED TREES	**ACTIVITY (N)**	
MALAGASY TREE	**MOVE**	**REST**
AZININA	2	
FAMELONA	1	1
HAZOMAINTY	1	1
LALOTINA	3	2
MAMPAY	5	1
MOLANGA	1	2
RARA	4	2
RAVINALA	2	
SOMOTRORANA		2
TSIMAMASATSOKINA	1	
VINTANONA	1	
VOANTALANINA BERAVINA	1	
VOAPAKA KELIRAVINA	2	1

SIFAKA GROUP 1 FREQUENTLY USED TREES	FOOD (N)					
MALAGASY TREE	FLOWERS	FRUIT	LEAVES	LIANNA FLOWERS	LIANNA FRUIT	LIANNA LEAVES
APANGA			5			
AZININA			4			
DONGAVELONA	1			1		1
HAZOAMBOVAHY		3			2	1
LIANNE			12			
MAMPAY			3			
RARA			3			
SOMOTRORANA		3	1			
TROVA KELIRAVINA			3			

EULEMUR 34 FREQUENTLY USED TREES	ACTIVITY (N)	
MALAGASY TREE	MOVE	REST
ANTAFONANA	2	3
ATAFANALA	1	2
AZININA	3	2
FAMELONA	2	
HAZOBOANGY	1	1
LIANNA		2
MAMPAY	3	1
RAMY	5	
RARA	3	
ROMENDAFA	1	1
TAVOLO FOTSY	2	1
TAVOLO MENA	3	
VINTANONA		2
ZANAMENA	2	

EULEMUR 34 FREQUENTLY USED TREES		FOOD (N)	
MALAGASY TREE	FLOWERS	FRUIT	LEAVES
ANTAFARA	4		
FAMELONA		4	1
HAZOBOANGY	2		
LIANNA		2	1
MAMPAY	2		2
MANDRESY		6	
SADOKA KELIRAVINA			4

SIFAKA 10 FREQUENTLY USED TREES	FOOD (N)			
MALAGASY TREE	FLOWERS	FRUIT	LEAVES	LIANNA LEAVES
ANTAFONANA			3	

HAZOAMBO		2		
HAZOAMBOVAHY			2	2
LIANNE		2	3	
MAMPAY			6	
RARA			2	
ROBANGA				2
ROMENDAFA			2	
SAMATA	2			
SOMOTRORANA			5	
TAVOLO FOTSY			1	
VOFONAKOHO	1		1	
VONGO BERAVINA			2	
ZAMBO			3	

SIFAKA GROUP 10 FREQUENTLY USED TREES	**ACTIVITY (N)**	
MALAGASY TREE	MOVE	REST
AFOPOTSY	1	1
ANTAFONANA	1	1
AZININA	5	2
HAZOAMBO	1	1
LALOTINA	4	
LIANNE	1	
MAMPAY	1	
OMBARY	1	1
RAMY	2	1
RARA	3	1
RAVINALA	2	
SOMOTRORANA		1
TARANTANA	5	
TAVOLO FOTSY	5	1
TROVA KELIRAVINA	2	1
VONGO KELIRAVINA	2	

INDRI 40 FREQUENTLY USED TREES	**ACTIVITY (N)**	
Malagasy Tree	MOVE	REST
ANTAFONANA	2	2
ANTAVARATRA		3
AZININA	5	3
FAMELONA	1	1
HAZOBOANGY	3	2
LALOTINA	9	1
LONGOTRA	1	2
MAMPAY	8	2
OMBARY	3	2
RAMY	4	4

RARA	6	3
RAVINALA	4	
ROTRA	1	1
SOMOTRORANA	1	1
TARANTANA	2	
TAVOLO FOTSY	3	2
TROVA	1	1
TROVA KELIRAVINA	1	2
TSIPATIKA		2
VOANTALANINA KELIRAVINA		1
VOAPAKA BERAVINA	1	2
ZANAMENA	2	3

INDRI 40	**FOOD (N)**		
MALAGASY TREE	FLOWERS	FRUIT	LEAVES
ANTAFONANA	1		3
ANTAVARATRA			3
AZININA			8
LONGOTRA			3
RARA			15
ROMDENDAFA		1	
TAVOLO FOTSY			8
TAVOLO MENA			2
VOAPAKA BERAVINA			2
ZAMBO			5

INDRI 50 FREQUENTLY USED TREES	**FOOD (N)**		
MALAGASY TREE	FLOWERS	FRUIT	LEAVES
ANTAFONANA	8		1
AZININA			4
AZININA BERAVINA			2
LONGOTRA			5
RARA		9	10
TAVOLO FOTSY	2		3
TAVOLO MENA			2

INDRI 50 FREQUENTLY USED TREES	**ACTIVITY (N)**	
MALAGASY TREE	MOVE	REST
AMPANA	2	
ARINA	1	1
AZININA	1	4
HAZOMAINTY		2
LOMBIRO	2	1
LONGOTRA		2
MAMPAY	2	2
MAROANDO	1	1

OMBARY	1	1
OMPA	1	1
RARA	1	3
TAVOLO FOTSY	5	

INDRI 14 FREQUENTLY USED TREES	**FOOD (N)**	
MALAGASY TREE	FLOWERS	LEAVES
ANTAFARA	1	1
ANTAFONANA		6
AZININA		7
LONGOTRA		2
MAMPAY		6
RARA		8
TAVOLO FOTSY		2
VINTANONA	2	

INDRI 14 FREQUENTLY USED TREES	**ACTIVITY (N)**	
MALAGASY TREE	MOVE	REST
AZININA	2	2
LALOTINA		1
LONGOTRA	2	1
MAMPAY	2	2
TAVOLO FOTSY	4	
TROVA	2	

INDRI 45 FREQUENTLY USED TREES	**FOOD (N)**		
MALAGASY TREE	BARK	FLOWERS	LEAVES
AZININA			2
LONGOTRA			3
RARA			5
TAVOLO FOTSY	1		4
TAVOLO MENA			2
TSIMAMASATSOKINA			2
VINTANONA		1	1
VOAPAKA BERAVINA			2
ZAMBO		1	3

INDRI 45 FREQUENTLY USED TREES	**ACTIVITY (N)**	
MALAGASY TREE	MOVE	REST
AFOMENA	3	
AZININA	1	3
LALOTINA	3	
MAMPAY		2
RARA	4	5
TARANTANA	2	2

TAVOLO FOTSY	3	2
VINTANONA	1	1
VOAPAKA BERAVINA		2
VOAPAKA KELIRAVINA	5	4
ZAMBO	2	

INDRI 55 FREQUENTLY USED TREES	**FOOD (N)**	
MALAGASY TREE	FRUIT	LEAVES
ANTAFONANA		6
AZININA		3
MAMPAY		4
RARA		10
TAVOLO FOTSY	1	8
TAVOLO MENA		2
VOAPAKA BERAVINA		3
VOAPAKA KELIRAVINA		3

INDRI 55 FREQUENTLY USED TREES	**ACTIVITY (N)**	
MALAGASY TREE	MOVE	REST
AFOMENA	2	
ANTAFONANA		5
FAMELONA	3	1
LALOTINA	2	1
LENDENA		2
LONGOTRA	1	2
MAMPAY	1	4
MENAVOZONA	2	1
OMBARY	2	
RARA	5	6
RAVINALA	2	
TAVOLO FOTSY	2	4
VOAPAKA BERAVINA		2
VOAPAKA KELIRAVINA	3	
VONGO	2	
ZANAMENA	1	1

ETHOGRAM AND SUBSTRATE SIZE AND ORIENTATION MEASUREMENTS

Type of Locomotion

Leaping: A movement in which the hindlimbs are used to propel an animal across a gap. This includes quadrupedal standing then leaping and vertical clinging and then leaping.

Climbing: A movement up or down a strongly oblique or vertical support or through irregular and intertwined small supports.

Quadrupedalism: A movement in which all four limbs move in a regular pattern above a support. This includes walking and running.

Quadrupedal suspensory movements: a movement where the body progresses below a support using 4 limbs.
Bridging: A movement where spatial gaps are crossed. First, the hands are stretched out to grab the new support and second, the rest of the body is stretched across and then pulled over to the new support.
Vertical Bounding: Short successive jump-clings upward along a vertical support

Postures

Sitting: To rest with the haunches lowered onto a supporting surface.
Sit Extend: To rest with the haunches lowered onto a supporting surface with the legs fully extend in front of the body with feet often grasping a vertical of oblique substrate.
Sit Tail Wrap: To rest with the haunches lowered onto a supporting surface with the tail wrapped around the front of the body and often over the adjacent shoulder.
Stand: To maintain an upright position on top of a support with legs extended (on all four limbs or bipedally).
Vertical cling: The animal grasps a vertical or strongly oblique substrate without supporting any of its weight on other branches.
Suspension: The animal hangs beneath a support suspended by two or more limbs. In lemurs, the most common suspensory posture is quadrupedal, bipedal, and tripedal (two feet and one hand) postures are also used.
Recline: To lie down on ventrum, side, or back.

Correlated behavior

Travel: Movement between a series of trees. Often will involve longer distances
Feed/Forage: Movements within a single tree
Rest: Inactivity
Groom Self: Clean, maintain one's body via licking, scratching, or use of a toothcomb
Groom Other: Clean, maintain another's body via licking, scratching, or use of a toothcomb

Substrate

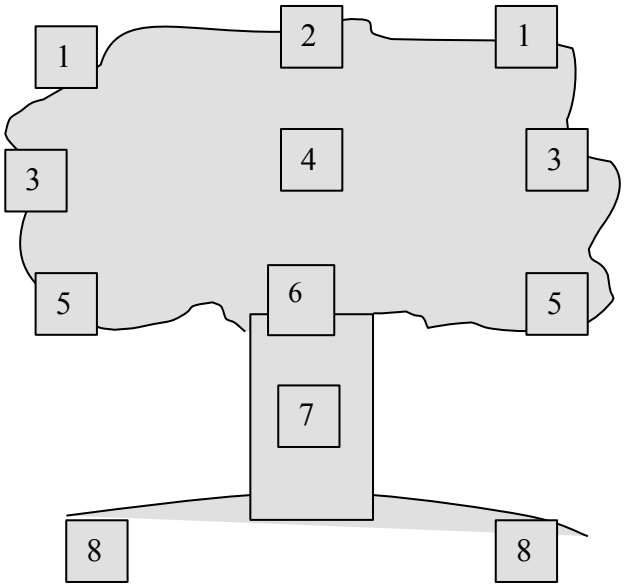
Support size: A, Very Small < 1cm; B, Small = 1-5cm; C, Medium 6-10cm; D, Large 11-15cm, E, Very Large 16+
Orientation: A, Horizontal (0-15 degrees); B, Oblique (15 to 75); C, Vertical (75-90).

Location

Height of substrate: A, 1m; B, 2-3m; C, 4-5m, D, 6m; E, 7-8m; F, 9-10m; G, 11m; H, 12-13m; I, 14-15m; J, 16+m

Connectedness

Canopy Distance: A, connected (0m); B, connected/small gaps; C, small gap (1-3m), D, small/medium gaps; E, medium gap (4-6m); F, large gap (7-9m); G, very large gap (>10m).



TREE QUADRANTS

MALAGASY COMMON AND LATIN NAMES OF TREES

APPENDIX TO MALAGASY AND LATIN NAMES	FAMILY	SPECIES
AZININA KELIRAVINA	CLUSIACEAE	SYMPHONIA LOUVELLI
LONGOTRA	LAURACEAE	ASPIDOSTEMON SPP
TAVOLO MENA	LAURACEAE	CRYPTOCARYA SP
AFOMENA	MALVACEAE	DOMBEYA SP
AMANINOMBILAHY	SARCOLENACEAE	LEPTOLAENA SP
AMBONAMBONA	ARALIACEAE	POLYSCIAS SP
AMPALIRANO	MORACEAE	FICUS SP
ANTAFARA	APOCYNACEAE	PETCHIA SP
ANTAFONANA	LAURACEAE	OCOTEA SP
ARINA	SARCOLENACEAE	RHODOLAENA SP
ATAFANALA	COMBRETACEAE	TERMINALIA SP
AZININA	CLUSIACEAE	SYMPHONIA SP
AZININA BERAVINA	CLUSIACEAE	SYMPHONIA SP
FAHAVALOTRAZO	RUTACEAE	ZANTHOXYLUM SP
FAMELONA	SAPOTACEAE	CHRYSOPHYLLUM SP
FANITOKAKOLAHY	FABACEAE	BAUHINIA HUMBLOTIANA
FANZANA	CYATHEACEAE	CYATHEA SPP
HASINA	CONVALLARICEAE	DRACAENA SP
HAZOAMBO	ANNONACEAE	XYLOPIAS SPP

HAZOBOANGY	EUPHORBIACEAE	SUREGADA SP
HAZOMAFANA	EBENACEAE	DIOSPYROS SPP
HAZOMAINTY	EBENACEAE	DIOSPYROS SPP
HAZOMAMY	ANISOPHYLEACEAE	ANYSOPHYLLEA FALLAX
HAZOMBOANGY	EUPHORBIACEAE	SUREGADA SP
HAZONDOMOINA	EUPHORBIACEAE	TANNODIA SP
LALOTINA	EUPHORBIACEAE	ANTHOSTEMA MADAGASCARIENSIS
LENDENA	GENTIANACEAE	ANTHOCLEISTA AMPLEXICAULIS
LONGOTRA	LAURACEAE	ASPIDOSTEMON SPP
MAMPAY	FABACEAE	CYNOMETRA SPP
MAROANDO	EUPHORBIACEAE	BLOTIA SP
MENAHIHY	ANACARDIACEAE	CAMPYLOSPERMUM SP
MENAVOZONA	ARECACEAE	DYPSIS LASTELLIANA
MOLANGA	MALVACEAE	DOMBEYA SP
OMBARY	ANNONACEAE	ISOLONA SP
OVOBOLA	ARECACEAE	ORIANA TRISPATHA
RAMY	BURSERACEAE	CANARIUM MADAGASCARIENSIS
RAVINALA	STRELITZIACEAE	RAVENALA MADAGASCARIENSIS
ROMENDAFA	SAPINDACEAE	TINOPSIS SP
ROTRA	MYRISTICEAE	SYZYGIUM SP
SADOKA	RUBIACEAE	GAERTHERA SP
SADOKA KELIRAVINA	RUBIACEAE	GAERTHERA SP
SAMATA	APOCYNACEAE	CERBERA MANGHAS
SOMOTRONANA	SAPINDACEAE	STADMANIA SP
TARANTANA	ANACARDIACEAE	MICHRONYCHIA MACROPHILIA
TAVOLO FOTSY	LAURACEAE	CRYPTOCARYA SP
TAVOLO MENA	LAURACEAE	CRYPTOCARYA SP
TAVOLO PIKA	LAURACEAE	CRYPTOCARYA SP
TROTROKA	MELASTOMACEAE	DICHAETANTHERA SP
TROVA BERAVINA	MORACEAE	TRECULIN SP
TSIMAMASATSOKINA	MELASTOMATACEAE	MEMECYLON SPP
TSIPATIKA	MORACEAE	STREBLUS SPP
VINTANONA	CLUSIACEAE	CALOPHYLLUM SP
VOALOHAKOHO	EUPHORBIACEAE	OMPHALEA OPPOSITITOLIA
VOANTALANINA	RUBIACEAE	ROTHMANNIA SP
VOANTALARINA KELIRAVINA	RUBIACEAE	ROTHMANNIA SP
VOAPAKA BERAVINA	EUPHORBIACEAE	UAPACA AMPLIFOLIA
VOAPAKA KELIRAVINA	EUPHORBIACEAE	UAPACA LOUVELLII
VOAPAKA MADIN'DINIRAVINA	EUPHORBIACEAE	UAPACA SP

VOASIRINDRINA	ANACARDIACEAE	SORENEA MADAGASCARIENSIS
VOLOMBORONA	FABACEAE	ALBIZIA GUMMIFERA
VONGO	CLUSIACEAE	RHEEDIA SPP
VONGO BERAVINA	CLUSIACEAE	RHEEDIA SPP
VONGO KELIRAVINA	EUPHORBIACEAE	UAPACA LOUVELLII
VONITRA	ARECACEAE	DYPSIS CRINATA
ZAMBO	CLUSIACEAE	MAMMEA BONGO
ZANAMENA	FABACEAE	DIALIUM UNIFOLIOLATUM

AVERAGE COUNTS OF ATTRIBUTES FROM QUANTIFIED PATCHES PER 100 SQUARE METERS

PATCH NAME	CANOPY COVER %	ELEVATION (M)	1 to 5 CM DBH/100M^2	6 to 10 CM DBH/100M^2	11 to 20 CM DBH/100M^2	21+ CM DBH/100M^2
GUAVA AVERAGE	70.7	350.0	9.8	6.3	1.2	1.6
ZUBENUBI AVERAGE	77.1	453.0	12.8	13.8	5.3	1.8
ZUBENUBI APRES AVERAGE	70.1	467.0	20.0	19.0	4.0	12.0
SAHAKOHO ADJACENT AVERAGE	72.0	416.0	20.0	19.0	5.0	4.0
SAHAKOHO AVERAGE	86.5	376.0	28.8	19.3	14.3	6.8
SAHABEFOZA AVERAGE	68.2	352.0	21.5	14.3	4.0	2.5
SAHABEFOZA AVANT AVERAGE	80.0	352.0	53.0	17.0	3.0	3.0
FARA AVERAGE	70.9	430.0	26.5	5.5	8.8	3.8
750/850 AVERAGE	69.8	390.0	45.0	38.0	1.0	1.0
800-900 AVERAGE	70.4	332.0	30.5	15.8	5.3	4.8
BETAKONONA AVERAGE	77.4	416.0	33.0	12.5	6.8	6.8
1600 AVERAGE	94.5	394.0	42.8	8.0	7.5	3.0

PATCH NAME	6 TO 10 CM DBH TRUNK DISTANCE (TD) (M)	11 TO 20 CM DBH TD (M)	21+ CM DBH TD (M)	6 TO 10 TRUNK SPATIAL PATTERN (SP)	11 TO 20 CM DBH SP	21+ CM DBH SP
GUAVA AVERAGE	<1 TO 2-3	3.8	1 to 3,4	EQUAL/CLUMPED	EQUAL	CLUMPED
ZUBENUBI AVERAGE	1 TO 3-4	1 TO 2	4.0	EQUAL	EQUAL/CLUMPED	EQUAL
ZUBENUBI APRES AVERAGE	<1	1 TO 3-4	<1 to 3-4	EQUAL	CLUMPED	CLUMPED
SAHAKOHO ADJACENT AVERAGE	<1	1.0	1.0	EQUAL	EQUAL	EQUAL
SAHAKOHO AVERAGE	<1	<1	1 TO 2	EQUAL	EQUAL	EQUAL
SAHABEFOZA AVERAGE	1.0	1 TO 2	2 TO 7	EQUAL	EQUAL	CLUMPED
SAHABEFOZA AVANT AVERAGE	<1	1 TO 2	<1 TO 3	EQUAL	EQUAL	CLUMPED
FARA AVERAGE	1 TO 3-4	1.0	1 TO 4-5	CLUMPED	EQUAL	CLUMPED
750/850 AVERAGE	1.0	<1 TO 10	<1 TO 10	EQUAL	CLUMPED	CLUMPED
800-900 AVERAGE	1.0	2 TO 3	1 TO 6	EQUAL	EQUAL/CLUMPED	CLUMPED
BETAKONONA AVERAGE	<1	1.0	1 TO 3-4	EQUAL	EQUAL	CLUMPED
1600 AVERAGE	1.0	1 TO 2-3	2 TO 4-5	EQUAL	EQUAL	EQUAL

PATCH NAME	HEIGHT 1 TOTAL CANOPY DISTANCE (TCD)	HEIGHT 2 TCD	HEIGHT 3 TCD	CANOPY HEIGHT 1 AVE (M)	CANOPY HEIGHT 2 AVE (M)	CANOPY HEIGHT 3 AVE (M)	CANOPY HEIGHT 4 AVE (M)
UAVA AVERAGE	A	F	F	3.7	4.6	8.3	0.0
UBENUBI AVERAGE	A	C	E	6.3	9.1	12.3	0.0
UBENUBI APRES AVERAGE	A	B	A	6.0	9.2	12.4	0.0
AHAKOHO ADJACENT AVERAGE	A	A	E	6.3	10.3	12.0	0.0
AHAKOHO AVERAGE	A	B	B	5.4	11.9	16.4	0.0
AHABEFOZA AVERAGE	A	A	E	3.5	7.4	11.4	0.0
AHABEFOZA AVANT AVERAGE	A	A	C	3.4	6.3	10.4	0.0
ARA AVERAGE	B	A	A	4.8	7.8	15.0	19.7
50/850 AVERAGE	A	A	E	3.8	6.3	0.0	0.0
00-900 AVERAGE	A	B	E	4.1	7.4	11.1	0.0
ETAKONONA AVERAGE	B	A	D	4.6	8.7	17.8	0.0
600 AVERAGE	A	B	E	5.2	9.4	14.0	0.0

PATCH NAME	NUMBER OF LONGOZA/100M^2	L0NGOZA ADJACENT TO PLOT	BAMBOO/ 100M^2	HERBS/ 100M^2	NEW GROWTH 0.3M/100M^2	NEW GROWTH 1.25 TO 1.9M/100M^2
GUAVA AVERAGE	0.0	0.0	0.0	6.2	1.4	1.6
ZUBENUBI AVERAGE	0.0	0.0	0.0	2.5	1.3	1.0
ZUBENUBI APRES AVERAGE	0.0	0.0	0.0	2.5	2.8	1.8
SAHAKOHO ADJACENT AVERAGE	0.0	0.5	0.0	1.5	4.5	3.5
SAHAKOHO AVERAGE	0.0	0.0	0.0	4.4	1.2	0.8
SAHABEFOZA AVERAGE	0.0	1.0	0.0	6.8	0.5	0.7
SAHABEFOZA AVANT AVERAGE	0.0	1.0	0.0	1.3	4.3	0.4
FARA AVERAGE	0.0	0.0	2.3	13.6	1.3	1.0
750/850 AVERAGE	0.0	0.0	0.0	1.0	2.0	1.1
800-900 AVERAGE	0.0	0.0	0.0	5.1	0.8	2.0
BETAKONONA AVERAGE	0.0	0.0	0.0	6.1	0.8	2.0
1600 AVERAGE	0.0	0.0	0.0	13.3	2.0	5.5

PATCH NAME	RAVINALA 100M^2	RAVINALA HEIGHT (M)	GUAVA TREES/100M^2	NEARBY STREAM?	DEAD STANDING TREES/100M^2	DEAD FALLEN TREES /100M^2
GUAVA AVERAGE	8.3	11.3	84.8	NO STREAM	1.5	1.0
ZUBENUBI AVERAGE	0.3	11.9	0.0	NO STREAM	0.8	4.5
ZUBENUBI APRES AVERAGE	0.2	0.0	0.0	NO STREAM	2.0	0.0
SAHAKOHO ADJACENT AVERAGE	0.0	0.0	0.0	NO STREAM	2.0	2.0
SAHAKOHO AVERAGE	3.0	11.3	2.0	NO STREAM	0.5	0.8
SAHABEFOZA AVERAGE	2.3	7.3	7.5	STREAM	0.0	0.3
SAHABEFOZA AVANT AVERAGE	0.0	0.0	0.0	STREAM	0.0	0.3
FARA AVERAGE	0.0	0.0	0.0	STREAM	2.3	3.8
750/850 AVERAGE	18.0	4.7	73.0	NO STREAM	0.8	0.8
800-900 AVERAGE	4.8	6.5	1.3	NO STREAM	0.0	0.3
BETAKONONA AVERAGE	0.0	0.0	0.0	NO STREAM	0.0	4.0
1600 AVERAGE	0.5	0.0	0.0	NO STREAM	0.0	1.0

PATCH NAME	SLOPE (DEGREES)	EMERGENT TREES/100M^2	EMERGENT TREE HEIGHT (M)	PALMS/ 100M^2	LIANA/ 100M^2
GUAVA AVERAGE	29.5	1.0	8.6	1.3	10.8
ZUBENUBI AVERAGE	24.3	1.0	20.3	0.8	110.0
ZUBENUBI APRES AVERAGE	25.0	0.0	0.0	3.0	64.0
SAHAKOHO ADJACENT AVERAGE	26.0	0.0	0.0	2.0	39.0
SAHAKOHO AVERAGE	24.0	0.3	20.3	1.6	21.0
SAHABEFOZA AVERAGE	13.5	0.8	14.1	2.0	16.5
SAHABEFOZA AVANT AVERAGE	36.0	0.0	0.0	6.3	6.0
FARA AVERAGE	32.8	1.0	31.3	4.0	10.3
750/850 AVERAGE	30.8	0.0	0.0	3.3	18.5
800-900 AVERAGE	27.3	1.0	15.7	0.8	25.0
BETAKONONA AVERAGE	32.0	0.0	0.0	0.0	11.0
1600 AVERAGE	20.0	1.3	15.6	0.0	42.0